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Da cooperação entre Max-Planck-Institut für Limnologie, Arbeitsgruppe Tropenökologie, Plön, Alemanha Oc., e Instituto Nacional de Pesquisas da Amazônia, Manaus — Amazonas, Brasil

Temporary fat storage, an adaptation of some fish species to the waterlevel fluctuations and related environmental changes of the Amazon river

by

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Abstract

Analysis of Amazonian freshwater fish exhibited great differences in water- and fat content. Migratory species which deposit huge amounts of eggs in a single spawning act accumulate at high water-level great amounts of fat in various parts of the body. Nonmigratory species which spawn small quantities of eggs several times per year show little or no seasonality in fat storage.

Fat storage is related to the energy requirements of the species and is considered a very successful strategy by which many Amazonian fish species survive drastic environmental and related food supply changes, which are a result of the great monomodal waterlevel fluctuations of the Amazon and its big tributaries.

Keywords: Fish, chemical composition, Amazon, floodplain, ecology.

This study is dedicated to Prof. Harald Sioli to commemorate his 75th birthday.

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1. Introduction

Seasonal changes in environmental parameters normally result in changes in behaviour and metabolism of organisms. In temperate regions fish show periods of increased activity during spring and summer, when spawning occurs and feeding and growth reach their maxima. During autumn and winter, resting periods prevail. Similar behavioral modifications have been reported from arid or semi-arid regions, where periodic water stress forces the organisms to adapt to favourable and unfavourable periods. Many cyprinodontid species for instance belong to the group of annual fishes, which are genetically so adapted to dry and wet periods, that they die after a defined life span even when water is supplied artificially.

In equatorial Amazonia there is little climatic seasonality. Daily temperature fluctuations exceed seasonal fluctuations, and day length varies little throughout the year. The atmospheric humidity is always high ($> 80\%$), but the rainfall periodicity varies such that big rivers, like the Amazon and its main tributaries show a pronounced monomodal flood-pattern, with an annual amplitude of 6 - 20 m. This regular flooding creates large floodplains beside the rivers and periodically modifies the habitats of aquatic and terrestrial organisms (JUNK 1984).

Fish respond principally by periodic migration and/or specific spawning and feeding behaviour. The economically most important species perform large migrations in enormous shoals called "piracema" by the native fisherman, who adapt their fishing practise to the migrating behaviour. Furthermore observation of the riverine population indicates that at certain periods some fish species are fat but at others they are lean. Indigenous customs include certain dietary taboos. The consumption of certain fish species is prohibited at particular times of the year or for certain periods of an individual's life, indicating possible observation that changes in the chemical composition of the fish meat, which may result in an indisposition of the consumer, can occur (SMITH 1979).

In fact, when the hydrological cycle has significant effects on fish behaviour, it is likely, that it also has an effect on the chemical composition of the fish itself, for instance in the relationship between water, fat, protein and ash. Fat accumulation has been already mentioned by various authors (LOWE-McCONNEL 1964; SMITH 1979; GOULDING 1980), however, data has only been given by GURGEL & FREITAS 1972; CASTELO 1979 and CARVALHO 1980, 1984. In the following paper additional data are presented and an attempt is made to interpret them in the light of environmental parameters and related changes in fish behaviour.

2. Methodology

Fish for analysis were caught near Manaus, or bought from local fishermen in Manaus market. They were stored on ice to avoid water loss. Analyses were made of skinned fish fillets and the whole fish, using different specimens. In some cases additional gonad analyses were carried out.

For analysis, the whole fish, both fillets of small fish, or one fillet of big ones, were ground several times to form a homogenized sample. Gonads were homogenized in a mortar.

5 g were used for analysis by an ULTRA-X analyzer. Water content was determined by drying the sample to constant dry weight at 110°C . Fat content was determined from the dried sample by repeated CCl_4 extraction to constant dry weight. Mineral salts were determined by ashing the sample at 600°C , adding 1 ml of $15\% \text{Mg}(\text{CH}_3\text{COOH})_2$. Proteins were calculated as difference between wet weight, and the water-, fat-, and ash content.

A detailed description of the method, and comparison with other methods e. g. Soxhlet and Stoldt-Weibull for fat extraction and Kjeldahl for protein is given by FLEMMING & DRECHSLER (1966) and DEUFEL (1972). Standard deviations of about $\pm 0.3 - 0.6\%$ compared to the other methods were reported by FLEMMING & DRECHSLER (1966). The ULTRA-X was selected because of its simplicity and its speed, allowing a greater number of samples to be analyzed in a given time.

3. Results

2548 fish belonging to 40 species, 32 genera and 16 families were analyzed.

4 species (sardinha comprida *Triportheus elongatus*, jaraqui escama grossa *Semaprochilodus insignis*, pescada branca *Plagioscion squamosissimus* and tucunaré açú *Cichla ocellaris*) were analyzed on a monthly basis over two years. 10 species were analyzed over a year (pacú branco *Mylossoma duriventris*, mapará *Hypophthalmus edentatus*, caparari *Pseudoplatystoma tigrinum*, surubim *Pseudoplatystoma fasciatum*, cuiú cuiú *Oxydoras niger*, acara açú *Astronotus ocellatus*, branquinha cabeça lisa *Potamorhina* cf. *altamazonica*, branquinha comum *Potamorhina latior* curimatã *Prochilodus nigricans* and aracú *Leporinus fasciatus*).

Gonads from 6 species were analyzed (jaraqui escama grossa *Semaprochilodus insignis*, sardinha comprida *Triportheus elongatus*, cubiu *Anodus melanopogon*, curimatã *Prochilodus nigricans*, branquinha cabeça lisa, *Potamorhina* cf. *altamazonica*).

Results will be presented according to the amount of data available for each species, those species with great fluctuations in the investigated parameters being first presented.

3.1. Sardinha comprida (*Triportheus elongatus*) Fam. Characidae, Subfam. Bryconinae

The sardinha comprida is an elongated herring-like fish, about 20 - 25 cm long, weighing 80 - 120 g. Several species of sardinhas occur in great quantities near Manaus. All can be considered omnivorous (ALMEIDA 1980). They are known to form shoals although their migratory pattern has been little studied. Eggs ripen simultaneously. Spawning occurs once a year beginning at the onset of rising waterlevel. Sardinhas sell well on the Manaus market, but they are not particularly important because only big specimens are considered suitable for human consumption.

Data are available for whole fish and fish fillets for 1978, and from July 1981 to February 1982 (Fig. 1, 2). The gonads were analyzed in March 1985 (Tab. 1).

Fat and water content of whole fish and fillets show pronounced seasonality. At rising and high waterlevel average fat content attains a maximum, about 20 % in the whole fish and 10 % in the fillet, while individual values may be even higher (25 % and 17 %

respectively). Water content during this period is at its lowest, at about 62 % and 70 % respectively. At low waterlevel, fat content decreases to about 4 % in the whole fish and about 1 % in fillets. Protein content varies between 15 - 20 % in whole fish also reaching highest average values at low waterlevel. The protein content of fillets varies only slightly, between 18 and 19 %. Ash content is rather stable, 1.5 % for whole fish and 0.5 % for fillets.

Throughout the year large standard deviations emphasize the great heterogeneity of fish analyzed. During the spawning season, there is a pronounced difference in water- and protein content between males and females when the whole fish is analyzed (Table 1). Due to their large gonads females have 6 % less water and 6 % more protein than males. Gonads correspond to about 14 % of the female body weight, whereas for the males, it contributes ~0.5 %. Water content of female gonads reaches about 58 %, protein content about 38 %, fat content about 2 % and ash content about 2 %. Fat content is similar in males and females. Fillets of both sexes show little difference in chemical composition.

Whereas in 1978 lean fish occurred over a long period (about 7 months) in 1981/82 this period was rather short (about 2 months only). There was a great difference in the hydrologic cycle in these years: the rise in waterlevel was rather slow in 1978 but very quick in 1982.

Tab. 1: Size, weight and chemical composition of mature sardinha comprida (*Triportheus elongatus*) whole, fillet and ♀ gonads. Month of capture: March 1985. n = 5 specimens for each category. ♂ gonads were not analyzed because of their small size.

	♀			♂	
	Total	Fillet	Gonads	Total	Fillet
Total length (cm)	22.8 ± 1.3	23.6 ± 1.3	—	20.6 ± 1.9	22.8 ± 0.8
Weight (g)	95 ± 14	100 ± 16	—	51 ± 16	69 ± 7
Water (%)	69.8 ± 1.8	77.7 ± 0.8	14.2 ± 2.8	76.2 ± 1.2	77.4 ± 0.8
Protein (%)	24.5 ± 1.2	19.2 ± 0.2	58.0 ± 2.5	19.3 ± 1.4	20.5 ± 0.8
Fat (%)	2.2 ± 0.4	2.0 ± 0.2	2.1 ± 0.7	2.0 ± 0.2	0.5 ± 0.3
Ash (%)	3.5 ± 0.4	1.0 ± 0.2	1.8 ± 0.1	2.6 ± 0.3	1.5 ± 0.2

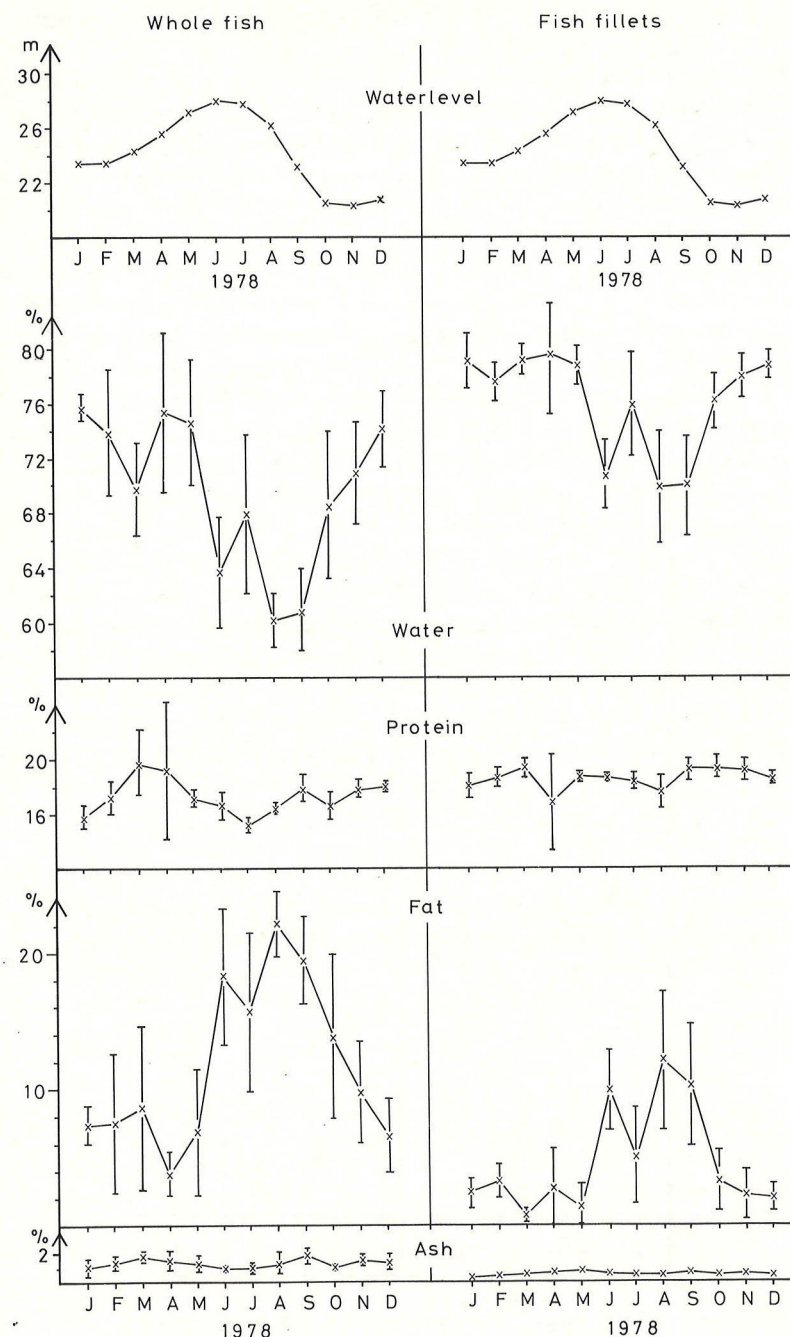


Fig. 1: Water-, protein-, fat- and ash content of the sardinha comprida (*Triportheus elongatus*) and its fillet in comparison with the waterlevel in 1978. (Whole fish: 24 ♂ 36 ♀; total length 15 - 28 cm, \bar{x} = 23.6 cm; weight 40 - 240 g, \bar{x} = 103 g. Fillet: 27 ♂ 33 ♀; total length 16 - 29 cm, \bar{x} = 23.8 cm; weight 30 - 220 g, \bar{x} = 108 g).

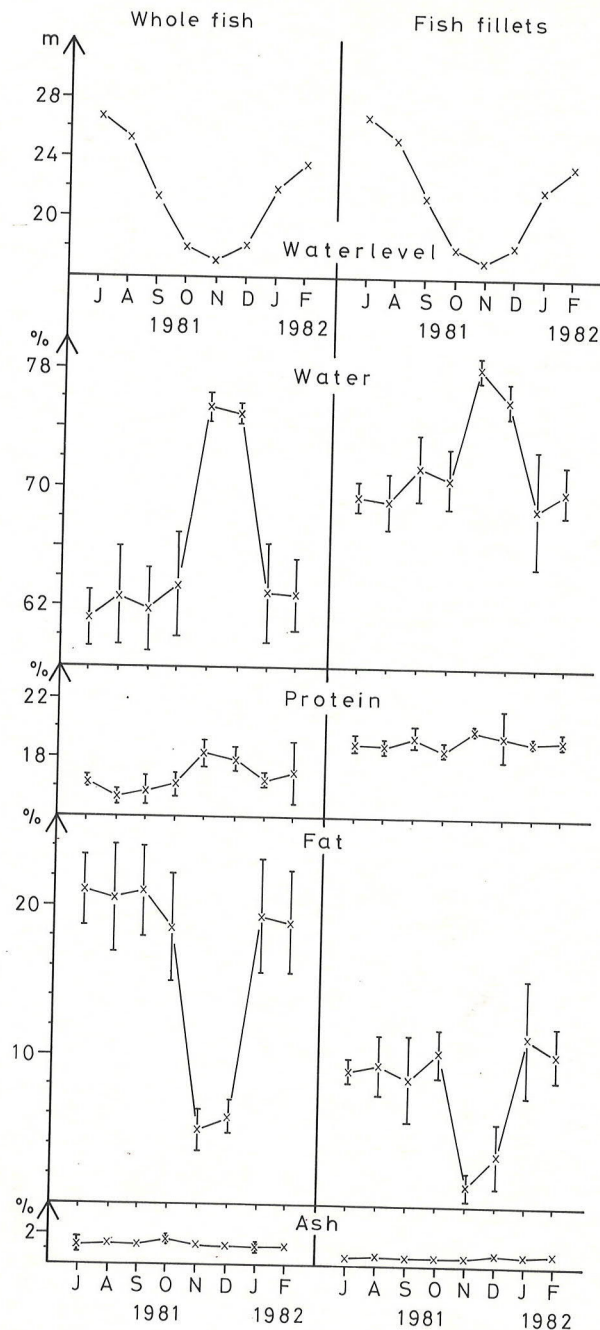


Fig. 2:
Water-, protein-, fat- and ash content of the sardinha comprida (*Triportheus elongatus*) and its fillet in comparison with the waterlevel in 1981/82. (Whole fish: 15 ♂ 25 ♀; total length 16 - 28 cm, \bar{x} = 23.8 cm; weight 45 - 230 g, \bar{x} = 99 g. Fillet: 14 ♂ 26 ♀; total length 17 - 28 cm, \bar{x} = 24.2 cm; weight 55 - 235 g, \bar{x} = 101 g).

3.2. Jaraqui escama grossa (*Semaprochilodus insignis*)* Fam. Curimatidae, Subfam. Prochilodinae

The jaraqui escama grossa is an elongated fish 25 - 30 cm long weighing 300 - 400 g. 2 similar species of jaraquis (*S. insignis*, *S. taeniurus*) occur in Central Amazonia in mixed shoals. The adults feed on fine detritus and periphyton in the flooded forest of blackwater tributaries. The migratory pattern is very complex and extend over distances of several hundred kilometres (RIBEIRO 1983). Eggs ripen simultaneously, spawning occurs once a year, beginning at the onset of rising waterlevel. Economically the jaraquis are the most important species, representing 40 % (16 000 t) of the total fish sold on the Manaus market, in 1984 (JUNK in press).

Data are available from January 1977 to January 1979 for whole fish, from January 1977 to February 1978 for fish fillets (Fig. 3, 4), and from January 1984 for gonads (Tab. 2).

Fat and water content of the whole fish and the fillets show pronounced seasonality. At high waterlevel fat content is highest, with average values of up to 15 % for whole fish and 6 % for fillets. Individual values can attain 16 % and 8 % respectively. Average water content during this period falls to 66 % and 74 % respectively. At low and rising water, fat content in the whole fish decrease to 1 % and in fillets to about 0.5 %. Water content of both increases to 80 %. Protein content varies slightly between 16 and 20 % in whole fish, reaching highest average values at low waterlevel. Individual values may reach 26 %. The protein content of fillets varies only little between 18 and 20 %. Ash content remains rather stable about 2 % in whole fish and 1 % in fillets.

Large standard deviations again emphasise the great heterogeneity between individuals. During spawning season, differences occur due to gonad size. In females gonads correspond to 17 % of the body weight, in males to less than 0.5 %. Female gonads have about 56 % water, 39 % protein, 4 % fat and 1 % ash content (Table 2).

Tab. 2: Size, weight and chemical composition of mature jaraqui escama grossa (*Semaprochilodus insignis*): whole, fillet and ♀ gonads. Month of capture: January 1984
n = 5 specimen for every category. ♂ gonads were not analyzed because of their small size (0.9 ± 0.1 g).

Mature fish	♀			♂	
	Total	Fillet	Gonads	Total	Fillet
Total length (cm)	28.3 ± 0.9	27.9 ± 2.4	—	27.6 ± 0.6	28.8 ± 0.6
Weight (g)	325 ± 13	354 ± 81	60.5 ± 11	302 ± 24	322 ± 19
Water (%)	75.6 ± 2.6	79.5 ± 0.8	55.7 ± 1.1	74.2 ± 0.8	77.8 ± 0.6
Protein (%)	20.9 ± 1.9	19.1 ± 0.5	39.0 ± 0.9	18.6 ± 1.0	20.7 ± 0.2
Fat (%)	1.6 ± 0.9	0.6 ± 0.4	4.1 ± 1.3	5.5 ± 1.1	0.5 ± 0.2
Ash (%)	1.8 ± 0.3	0.8 ± 0.2	1.2 ± 0.2	1.7 ± 0.4	1.0 ± 0.3

* In some papers the jaraqui escama grossa is also called *S. theraponura*.

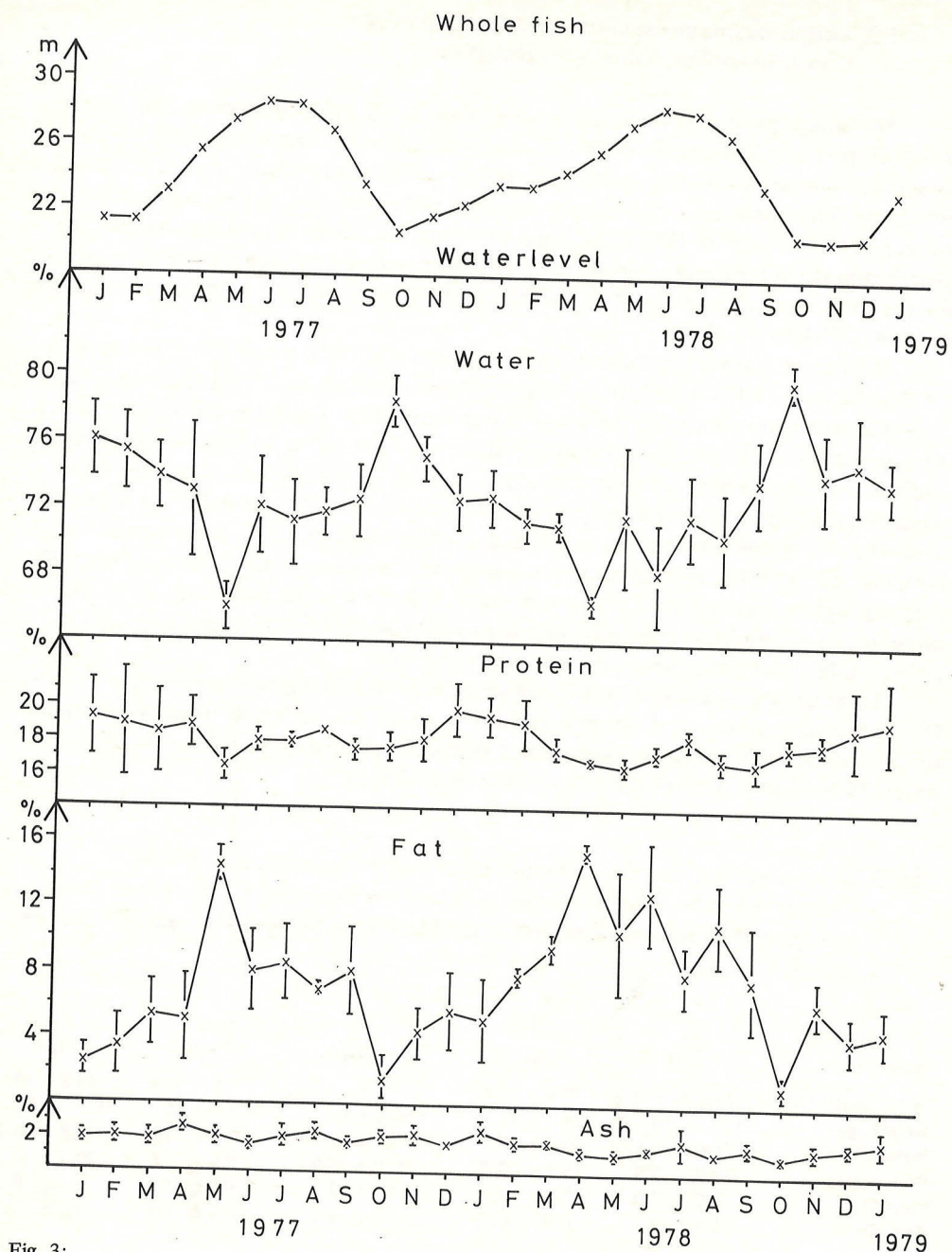


Fig. 3:
Water-, protein-, fat- and ash content of the jaraqui escama grossa (*Semaprochilodus insignis*) in comparison with the waterlevel in 1977/78. (44 ♂ 76 ♀; total length 22 - 31 cm, \bar{x} = 27.5 cm; weight 120 - 930 g, \bar{x} = 319 g).

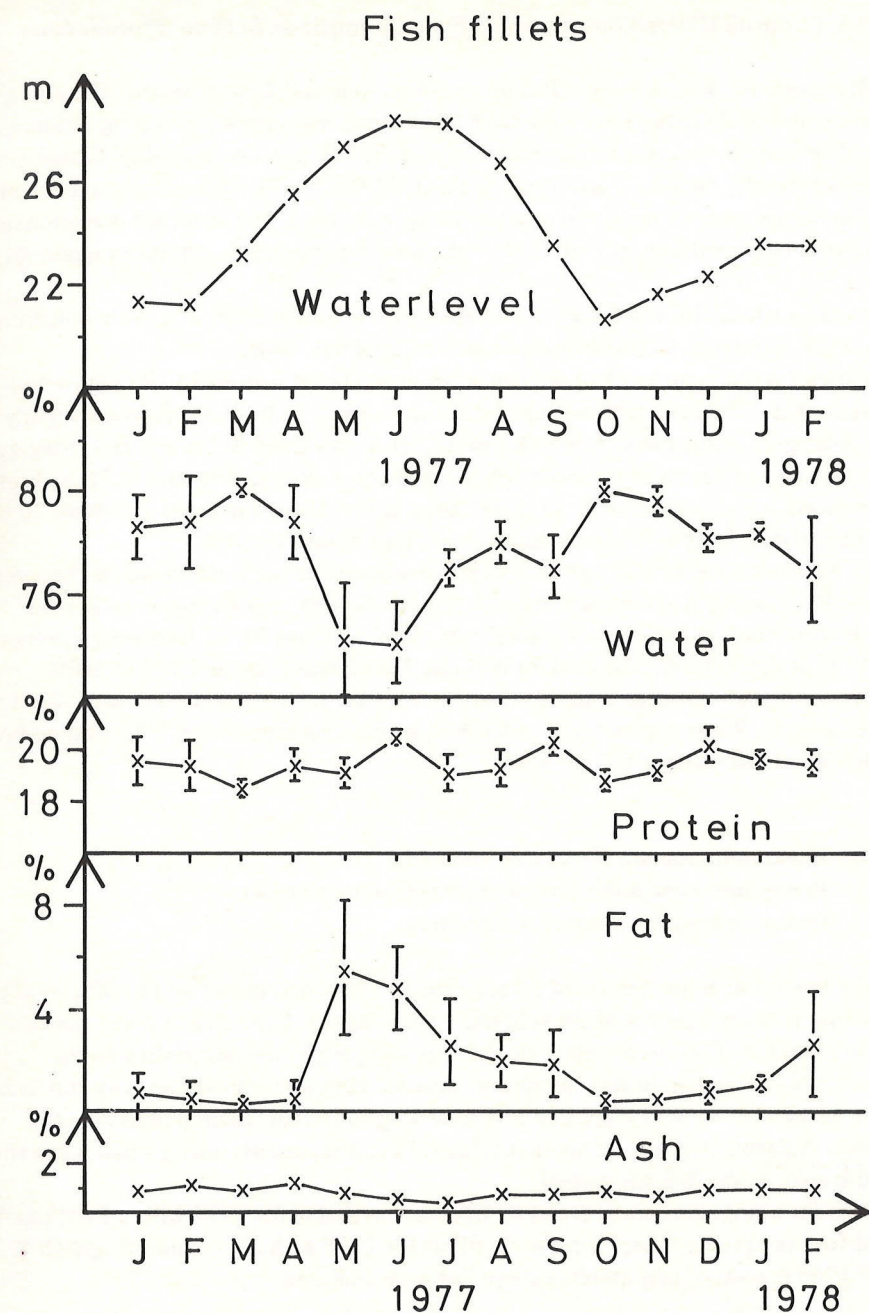


Fig. 4:
Water-, protein-, fat- and ash content of the fillet of the jaraqui escama grossa (*Semaprochilodus insignis*) in comparison with the waterlevel in 1977/78. (28 ♂ 42 ♀; total length 22 - 36 cm, \bar{x} = 31.8 cm, weight 160 - 920 g, \bar{x} = 369 g).

3.3. Curimatã (*Prochilodus nigricans*) Fam. Curimatidae, Subfam. Prochilodinae

The curimatã is an elongated fish up to 60 cm long and 2 kg in weight. The adults feed on detritus and periphyton. They form large shoals and migrate over long distances. A related species *Prochilodus scrofa*, migrates over 1000 km in the river Mogi-Guaçu a tributary of the Rio Grande in São Paulo State (GODOY 1967). Eggs ripen simultaneously. Spawning occurs once a year at the onset of rising waterlevel. The curimatã is economically very important, contributing about 12 % of the total fish sold in the Manaus market (JUNK in press).

Data on whole fish and fillet are available for 1977 apart from May, July and November for whole fish (Fig. 5). Gonads were analyzed in March 1985.

Fat and water content of whole fish show pronounced seasonality. At high water-level fat content is highest, with average values up to 18 %. Individual values are slightly higher. Average water content during this period decreases to 64 %. At low and rising water average fat content decreases to about 3 % and average water content rises to 78 %. Protein content shows a slight seasonality. Average values at low and rising water are about 20 % and at high water about 17 %. Individual values range from 15 - 24 %.

In fillets seasonality fluctuation is slight. Average water content fluctuates between 76 % and 82 % and fat content between 0.5 % and 4 %, with slightly higher individual values. Protein content maintains a rather stable level at about 20 %, decreasing briefly to about 17 % at rising water. Ash content is about 3 % in whole fish and 1 % in fillets.

Female gonads are large comprising about 15 % of the body weight of an $890 \text{ g} \pm 57$ specimen ($n = 5$). Water content is $57.8 \pm 0.8 \%$, protein content $38.2 \pm 2.8 \%$, fat content $2.3 \pm 0.9 \%$ and ash content $1.7 \pm 0.3 \%$.

3.4. Branquinha comum (*Potamorhina latior*)

Branquinha cabeça lisa (*Potamorhina cf. altamazonica*)

Fam. Curimatidae, Subfam. Curimatinae

The branquinhas are elongated silvery fish, 15 - 35 cm long and up to 500 g in weight. They belong to several genera of the subfamily Curimatinae. More than a dozen species occur near Manaus. They feed mainly on detritus and periphyton. According to the fishermen, they all belong to the "piracema" species. Eggs ripen simultaneously. Little is, however, known about their migration and spawning behaviour. Branquinhas are very frequent in Amazonian rivers. Its market value is low; it represents only a small proportion of the fish sold on the Manaus market.

Data for branquinha comum and its fillets are available for 1977 with a 2 (3) month gap, and for branquinha cabeça lisa and its fillets for 1978 with a 3 (2) month gap (Fig. 7). In April 1985 gonads of branquinha cabeça lisa were analyzed.

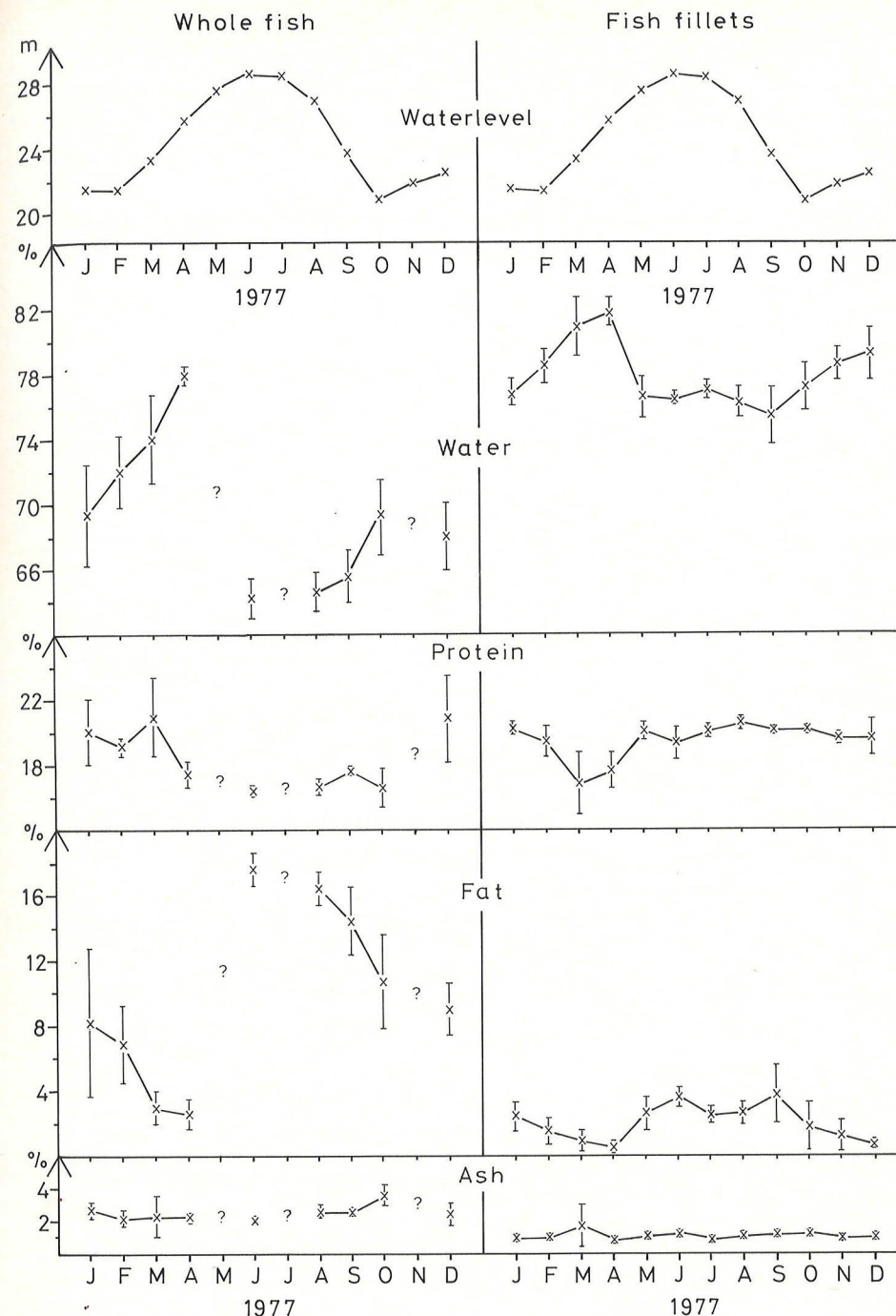


Fig. 5:

Water-, protein-, fat- and ash content of the curimatã (*Prochilodus nigricans*) and its fillet in comparison with the waterlevel in 1977. (Whole fish: 18 ♂ 27 ♀; total length 28 - 47 cm, $\bar{x} = 36.4$ cm; weight 360 - 1500 g, $\bar{x} = 795$ g. Fillet: 23 ♂ 37 ♀; total length 27 - 48 cm, $\bar{x} = 35.4$ cm, weight 330 - 1530 g, $\bar{x} = 727$ g).

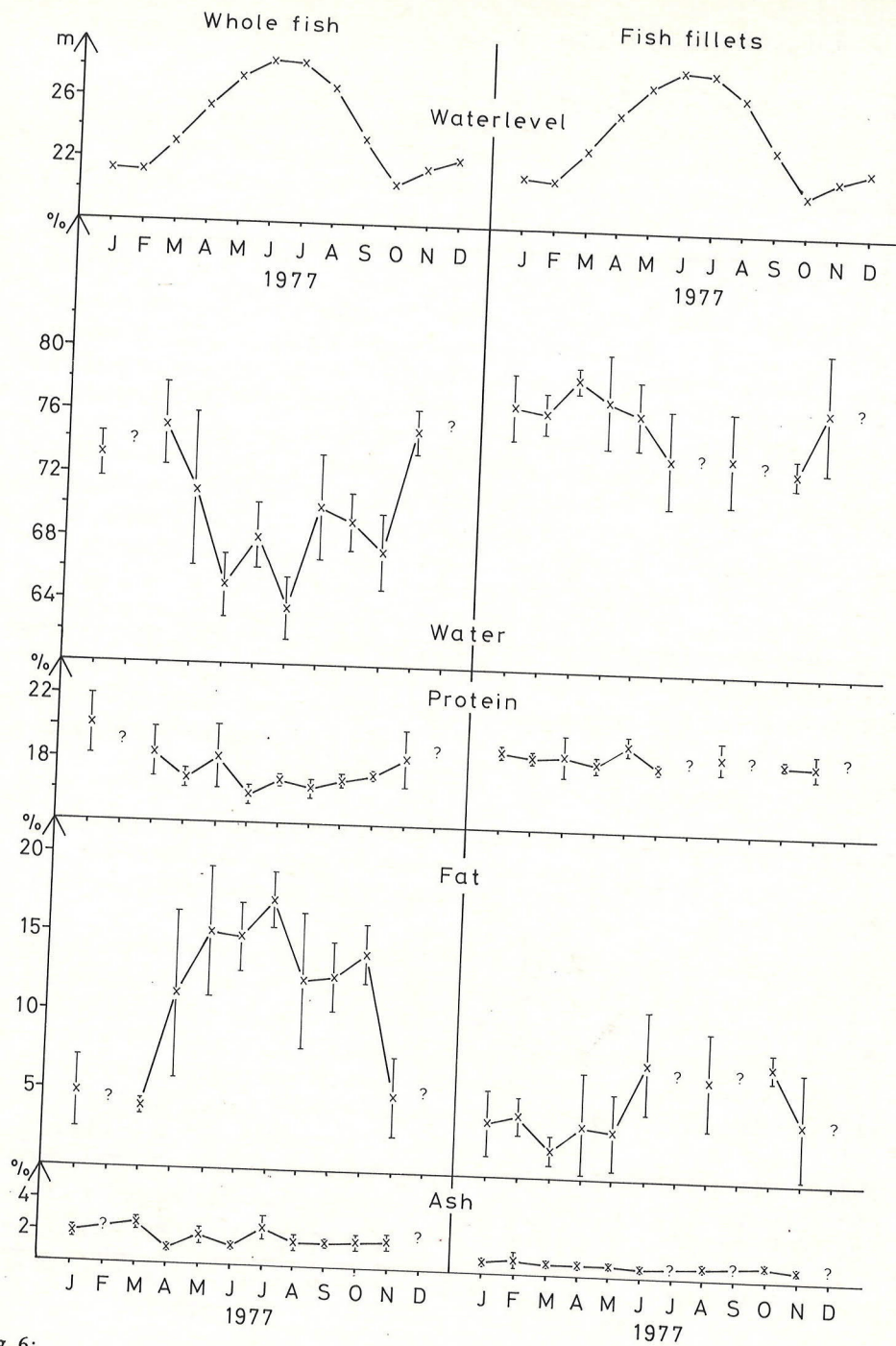


Fig. 6:
Water, protein, fat- and ash content of the branquinha comum (*Potamorhina latior*) and its fillet in comparison with the waterlevel in 1977. (Whole fish: 40 ♂ 10 ♀; total length 19 - 32 cm, \bar{x} = 23.5 cm; weight 70 - 410 g, \bar{x} = 188 g. Fillet 8 ♂ 37 ♀; total length 18 - 33 cm, \bar{x} = 24.4 cm; weight 90 - 530 g, \bar{x} = 223 g).

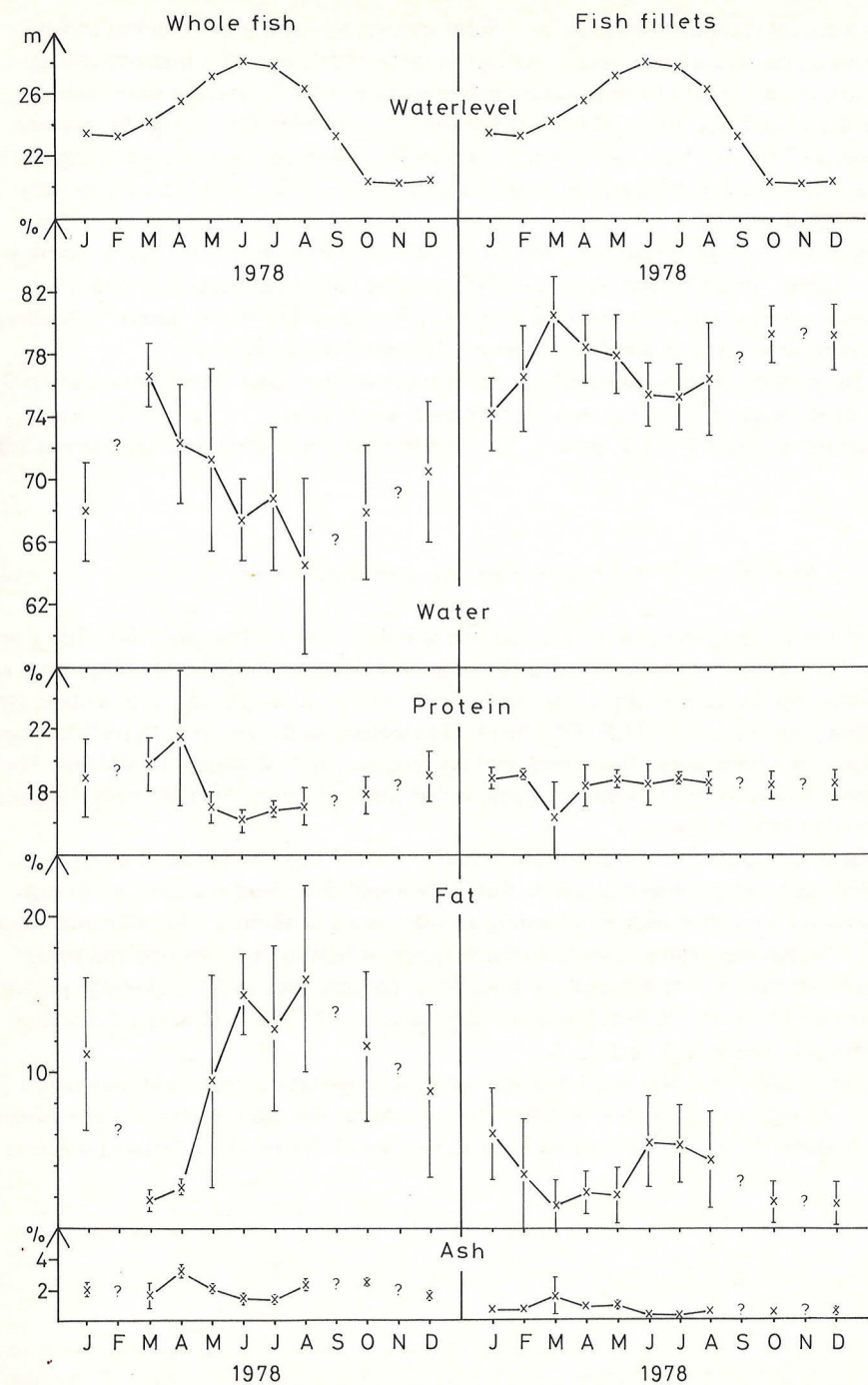


Fig. 7:
Water, protein, fat- and ash content of the branquinha cabeça lisa (*Potamorhina cf. altamazonica*) and its fillet in comparison with the waterlevel in 1978. (Whole fish: 18 ♂ 27 ♀; total length 20 - 31 cm, \bar{x} = 26.8 cm, weight 100 - 450 g, \bar{x} = 246 g. Fillet: 24 ♂ 26 ♀; total length 22 - 32 cm, \bar{x} = 27.9 cm, weight 140 - 560 g, \bar{x} = 317 g).

Chemical composition is similar in both species. Fat- and water content of whole fish show a pronounced seasonality. At high waterlevel fat content is highest, average values attaining 17 %. Individual values may even exceed 20 %. Average water content during this period falls to about 64 %. At low and rising waterlevel average fat content decreases to 2 % - 4 % but water content rises to 76 %. Average protein level is slightly increased at low water (20 %) but decreases at high water (16 %). Individual values vary between 15 % and 24 %.

Similar, although much less pronounced differences are found for fillets. Average water content varies between 74 % and 80 %, and fat content between 2 % and 8 %. Individual values reach 10 %. Average protein content is rather stable, about 19 %. Average ash content of whole fish and fillets is about 2 % and 0.8 % respectively.

The gonads of branquinha cabeça lisa females are very large, representing about 21 % of the total weight of 21 ± 1.0 cm long specimen weighing 137 ± 11 g ($n = 5$). Gonad water content is $61.4 \% \pm 1.1$, protein $33.2 \% \pm 0.9$, fat $3.6 \% \pm 1.1$ and ash content $1.8 \% \pm 0.2$.

3.5. Aracú (*Leporinus fasciatus*) Fam. Anostomidae

The aracú is an elongated, cylindric fish about 25 - 35 cm long and 400 - 700 g in weight. Several species belonging to different genera occur around Manaus (*Leporinus* spp. *Rhytidodus* spp. *Schizodon* spp.). The adults feed mainly on periphyton, filamentous algae and aquatic macrophytes (SANTOS 1981). They belong to the group of "piracema" species. Eggs ripen simultaneously. The aracús are very frequent in Amazonian floodplains. They contribute relatively little to the total amount of fish sold on the Manaus market because their market value is low.

Data for whole fish and fillets are available for 1978 except March (Fig. 8).

Fat- and water content of whole fish show a well developed seasonality. At high waterlevel fat content is highest, attaining average values of about 15 %. Individual values attain 17 %. Average water content during this period falls to 66 %. At low and rising water average fat content decreases to 6 %. Water content rises to 72 %. Average protein content varies between 20 % at low and rising water and 17 % at high water, individual values lying between 16 % and 22 %.

Fluctuations in fillets are less pronounced. Average fat content varies between 1 % and 5 %, average water content between 75 % and 80 %. Average protein content remains stable at about 20 %. Ash content is rather stable, about 2 % in whole fish and 0.8 % in fillets.

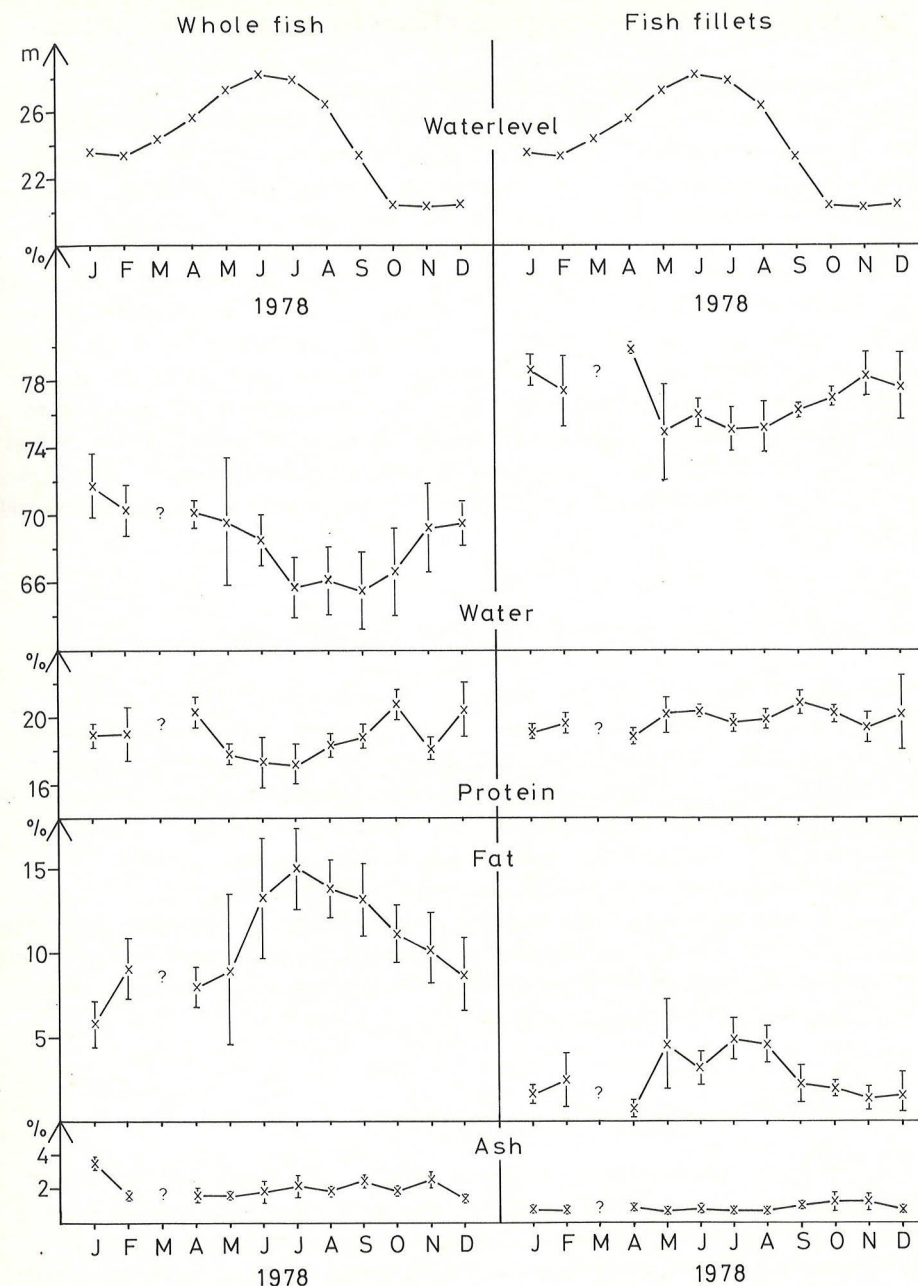


Fig. 8: Water-, protein-, fat-, and ash content of the aracú (*Leporinus fasciatus*) and its fillet in comparison with the waterlevel in 1978. (Whole fish: 25 ♂ 30 ♀; total length 24 - 36 cm, $\bar{x} = 29.3$ cm; weight 180 - 650 g, $\bar{x} = 362$ g. Fillet: 21 ♂ 34 ♀; total length 24 - 41 cm, $\bar{x} = 31.2$ cm; weight 200 - 690 g, $\bar{x} = 402$ g).

3.6. Pacú branco (*Mylossoma duriventris*) Fam. Serrasalminae, Subfam. Myleinae

The pacú branco is a disc-like fish about 20 - 25 cm long weighing 200 - 350 g. It feeds on fruit and seeds from the flooded forest in addition to aquatic macrophytes, periphyton, terrestrial and aquatic invertebrates (PAIXÃO 1980). Pacús are known to form shoals and to migrate. Eggs ripen simultaneously. They are important and highly prized commercial fish. Several species are sold on the Manaus market.

Data for the whole fish and fillets are available for 1978 (except June) (Fig. 9).

Fat and water content of the whole fish and fillets show pronounced seasonality. At peak flood fat content is highest, with average values of 28 % in whole fish and 12 % in fillets. Individual values attain 32 % and 19 % respectively. During that period average water content decreases to 55 % and 72 % respectively. At low water, average fat content decreases to 10 % in whole fish and 2 % in fillets, whereas average water content rises to 72 % and 80 % respectively. Average protein content of whole fish varies between 19 % at low water and 15 % at high water. The protein content of the fillets varies between 17 % and 0.8 % in fillets.

3.7. Mapará (*Hypophthalmus edentatus*) Fam. Hypophthalmidae

The mapará is a plankton-feeding pelagic catfish up to 60 cm long and 2000 g in weight. Several species occur in the Amazon basin. *Hypophthalmus perporosus* is known to form large shoals in the Tocantins river and perform migrations. Eggs ripen simultaneously. CARVALHO (1980) suggests that near Manaus spawning behaviour in *Hypophthalmus edentatus* is similar but its migratory behaviour remains poorly studied. The species is rarely found on the Manaus market because its flesh is soft and fat.

Chemical composition data for 1977 are available for fillets (Fig. 10).

Fat and water content show very strong seasonal variation. At high water, fat content is highest, up to 32 %, whereas water content during the period decreases to 56 %. Protein and ash content vary little, approximately 15 % and 0.5 % respectively. Protein content is lowest at high water, when the fish is very fat.

3.8. Cuiú cuiú (*Oxydoras niger*) Fam. Doradidae

The cuiú cuiú is a bottom-living, toothless catfish of more than 1 m length and up to 20 kg weight. It feeds on detritus and benthic animals. It is known to migrate in the Madeira river (GOULDING 1980), but its migratory and spawning behaviour remains poorly known. The species is rarely found on the Manaus market because its flesh is little appreciated.

Chemical composition data on fillets are available for 1979 (Table 3). Water content fluctuates between 81 % and 83 % and protein content between 16 % and 18 %. Fat content is about 0.4 % and ash content about 0.6 %. Water-, fat-, protein- and ash content show no clear annual seasonality.

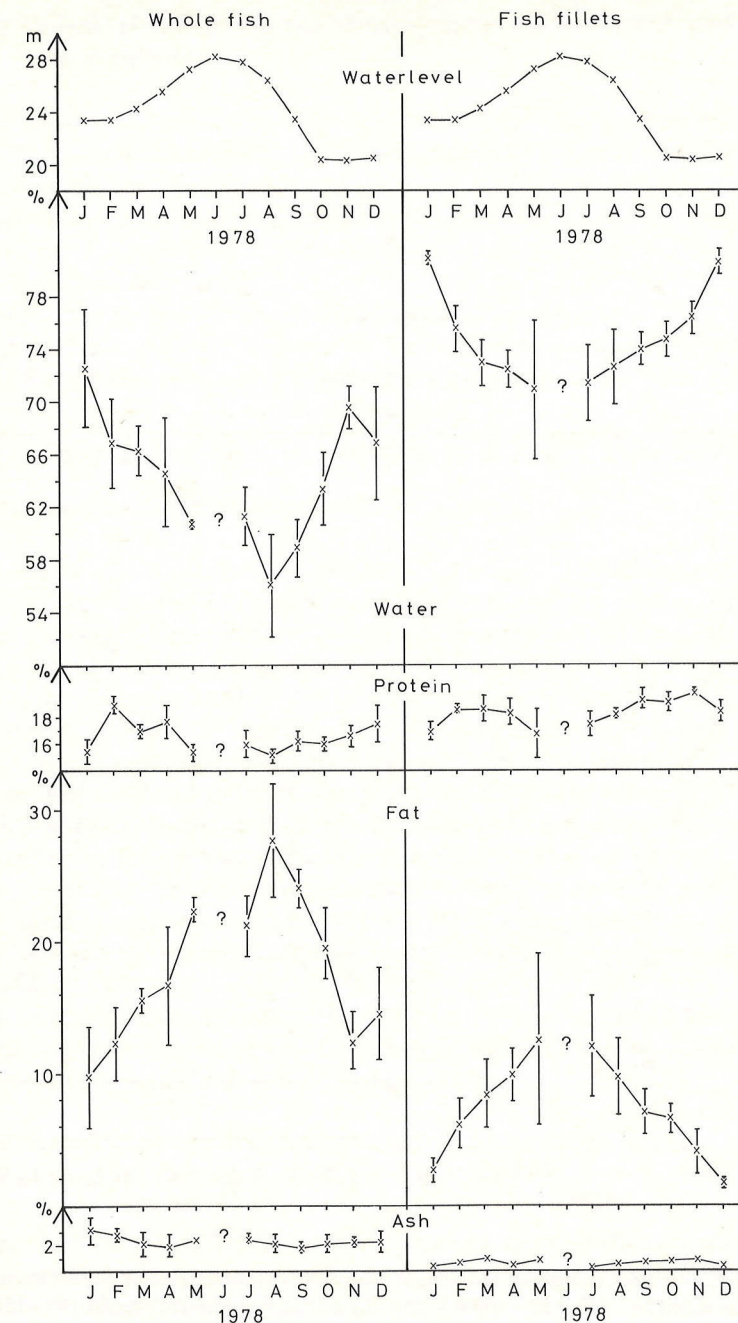


Fig. 9:
Water-, protein-, fat- and ash content of the pacú branco (*Mylossoma duriventris*) and its fillet in comparison with the waterlevel in 1978. (Whole fish: 10 ♂ 45 ♀; total length 15 - 25 cm, \bar{x} = 18.7 cm; weight 90 - 350 g, \bar{x} = 177 g, Fillet: 5 ♂ 50 ♀; total length 14 - 23 cm, \bar{x} = 18.9 cm; weight 75 - 380 g, \bar{x} = 194 g).

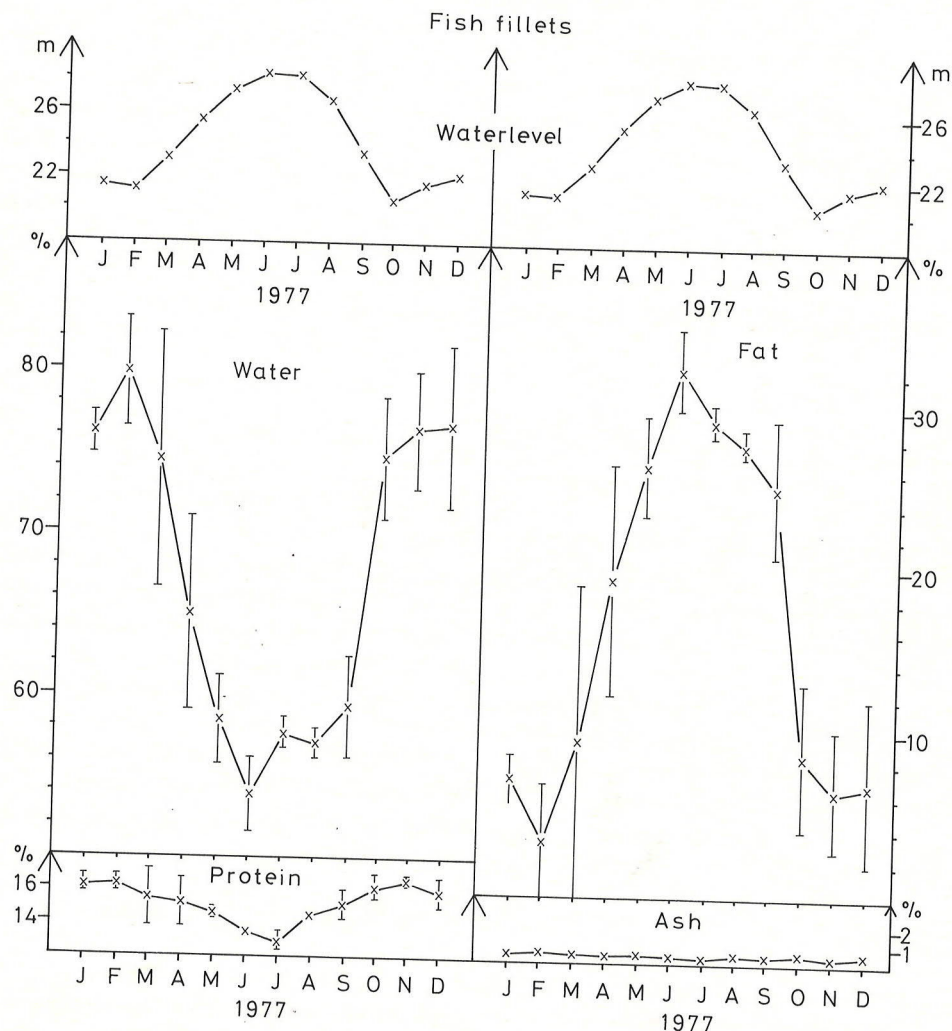


Fig. 10: Water-, protein-, fat- and ash content of the fillet of mapará (*Hypophthalmus edentatus*) in comparison with the waterlevel in 1977. (23 ♂ 37 ♀; total length 26 - 55 cm, \bar{x} = 43.6 cm; weight 180 - 1500 g, \bar{x} = 647 g).

3.9. Caparari (*Pseudoplatystoma tigrinum*) surubim (*Pseudoplatystoma fasciatum*) Fam. Pimelodidae

The caparari and the suburim are elongated bottom-living carnivorous catfish. They can attain 1.5 m length and 20 kg weight. According to GOULDING (1980) the species form shoals in the Rio Madeira and migrate upriver. There is, however, very little information about the migratory and spawning behaviour. Despite a general reluctance by the Central Amazonian population to consume catfish, small quantities of caparari and surubim are sold on the Manaus market.

Data on fillets are available for 1979 (Fig. 11, Table 3).

Water content fluctuates between 80 % and 82 % and protein content between 17 % and 19 %. Fat content is about 0.5 % and ash content about 0.8 %. Water-, fat-, protein- and ash content show no clear annual seasonality.

3.10. Tucunaré açú (*Cichla ocellaris*) Fam. Cichlidae

The tucunaré açú is a voracious predator which can attain 1 m in length and weight more than 10 kg. However it is usually much smaller. It does not migrate. When the water rises male and female form couples. They defend their territory and take care of the juveniles. Eggs ripen in batches and spawning can occur several times in a year, from the onset of rising water until peak flood or later. 2 species with similar behaviour occur frequently near Manaus (*C. ocellaris*, *C. temensis*). They are highly prized market species and renowned game; the amount available on the market is low (< 3 % of the total catch).

Data from 1977 and 1978 are available for whole fish and fillets (Fig. 12).

Fat and water content of whole fish fluctuate moderately throughout the year. At falling and low waterlevel, average fat content is highest attaining values of 5 %. Average water content during this period decreases to 74 %. At rising water, fat content decreases to 0.5 %, whereas water content increases up to 80 %. Average protein content fluctuates between 17 % and 19 % without any pronounced seasonality. Average ash content remains rather stable at 3 %.

Average water content in the fillets is 82 % at rising water and 78 % at low water, whereas average protein content rises from 17 % to 20 %. Fat content is 0.1 % and may rise to 0.5 % at low water. Ash content is about 0.8 %.

3.11. Acará açú (*Astronotus ocellatus*) Fam. Cichlidae

The acará açú is a cichlid, about 40 cm long and up to 1000 g in weight, which chiefly feeds on terrestrial and aquatic invertebrates. It is a non-migratory species with territorial behaviour and parental care for eggs and juveniles. Eggs ripen in batches and spawning can occur several times in a year, from the onset of rising water until peak flood, or later. It is a highly prized market species and, in the North-East of Brasil, is cultivated for human consumption.

Data for 1977 (except August) are available for whole fish and fillets (Fig. 13).

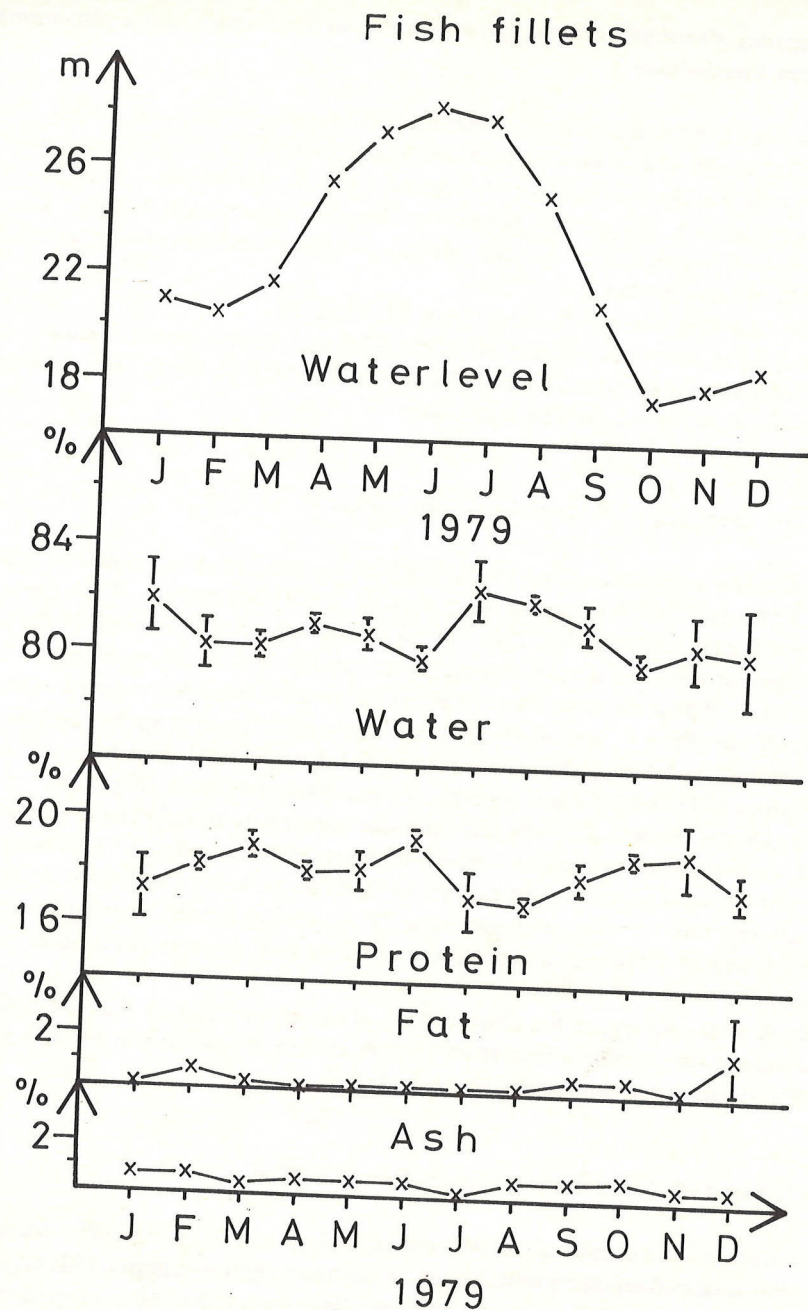


Fig. 11: Water-, protein-, fat- and ash content of the fillet of caparari (*Pseudoplatystoma tigrinum*) in comparison with the waterlevel in 1979. (26 ♂ 34 ♀; total length 36 - 93 cm, \bar{x} = 58.7 cm, weight 360 - 7050 g, \bar{x} = 1773 g).

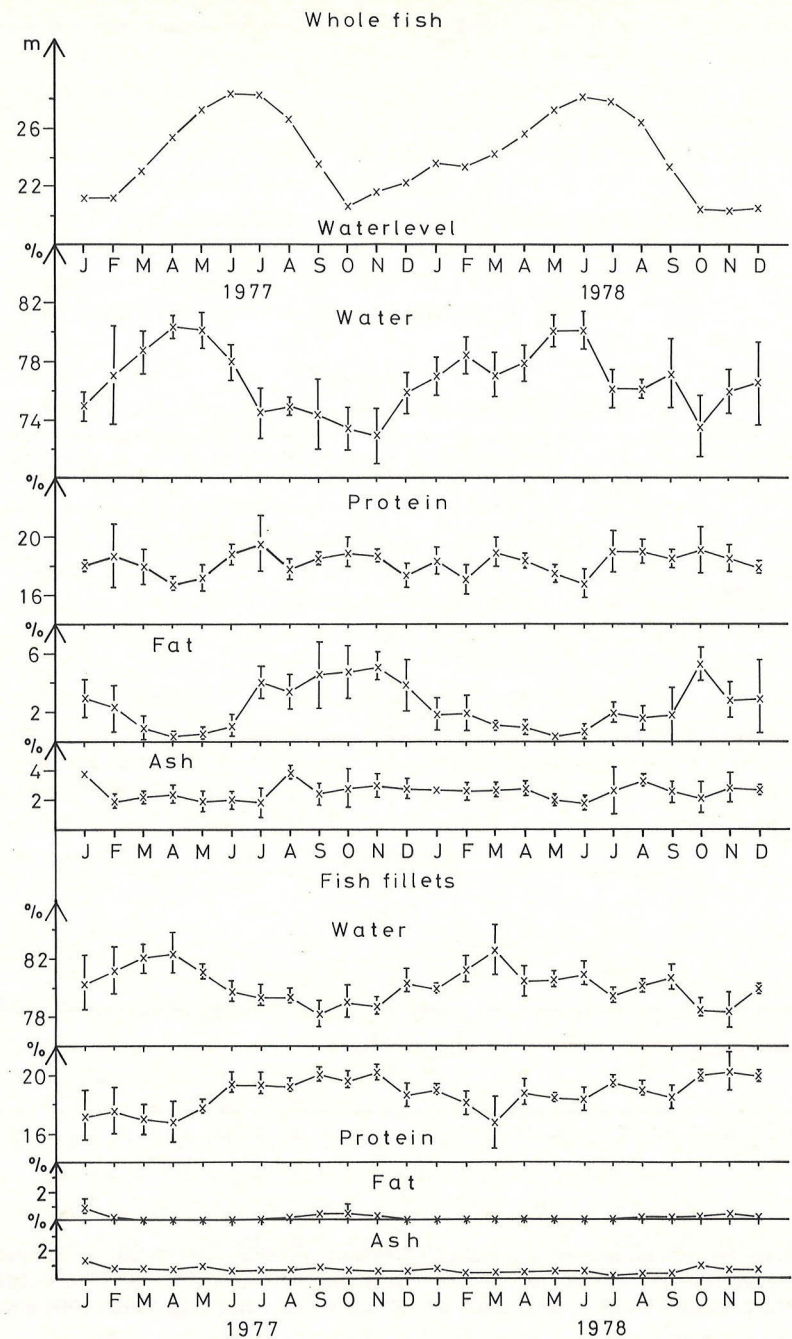


Fig. 12: Water-, protein-, fat- and ash content of tucunaré açu (*Cichla ocellaris*) and its fillet in comparison with the waterlevel in 1977/78. (Whole fish: 51 ♂ 69 ♀; total length 23 - 38 cm, \bar{x} = 30.0 cm; weight 140 - 850 g, \bar{x} = 408 g. Fillet: 50 ♂ 70 ♀; total length 28 - 48 cm, \bar{x} = 32.8 cm; weight 230 - 1800 g, \bar{x} = 549 g).

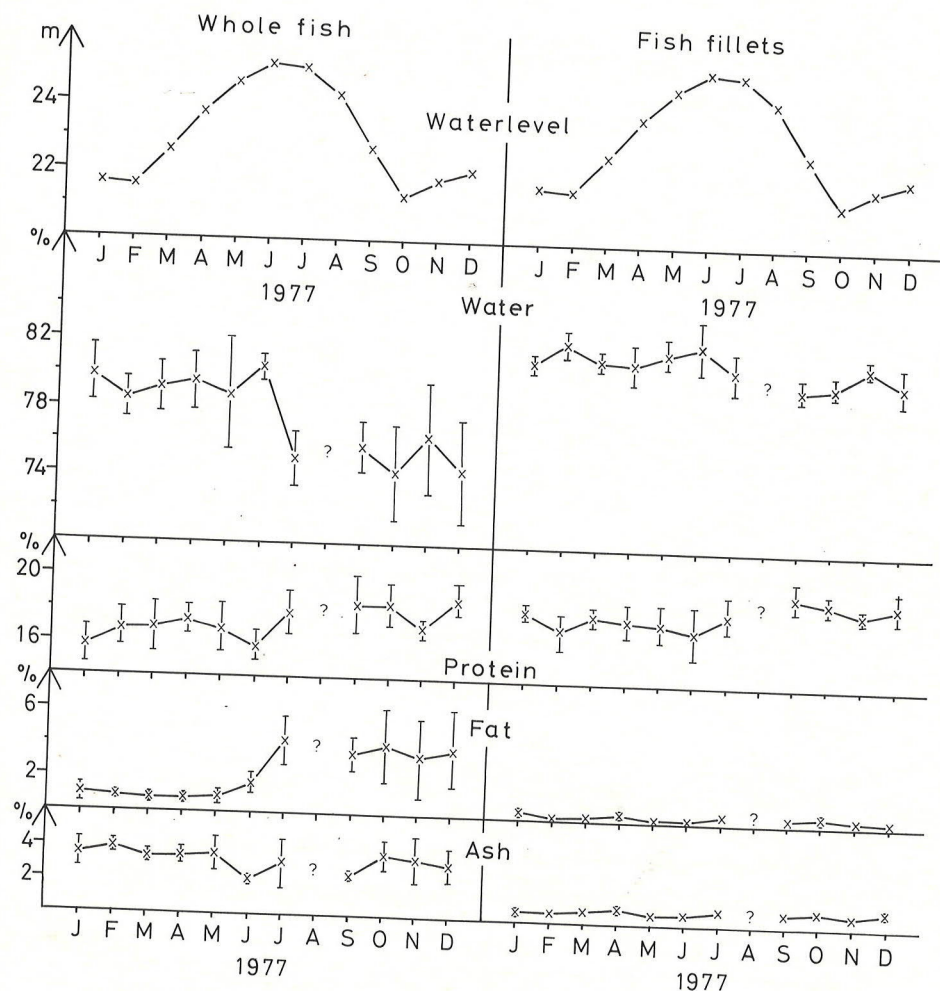


Fig. 13:
Water-, protein-, fat- and ash content of acará-açu (*Astronotus ocellatus*) and its fillet in comparison with the waterlevel in 1977. (Whole fish: 19 ♂ 36 ♀; total length 23 - 37 cm, \bar{x} = 27.1 cm; weight 300 - 900 g, \bar{x} = 460 g. Fillet: 19 ♂ 26 ♀; total length 23 - 37 cm, \bar{x} = 28.1 cm; weight 290 - 1000 g, \bar{x} = 531 g).

Fat and water content of whole fish show a slight seasonality. The average fat content is about 1 % at low and rising water, until peak flood in June, when it rises to approximately 4 %. Individual values may attain 6 %. The average water content drops from 80 % to 74 %, individual values varying between 71 and 82 %. Average protein content of whole fish shows a slight increase, from about 16 % at rising and high water to 18 % at falling and low water whereas ash content remained stable at about 3 %.

Variation in water and protein content of fillets is very slight. Average water content is highest at rising and high waterlevel and decreases from 82 % to 80 % with falling water. Average protein content rises from 17 % to 19 % over the same period. Fat and ash content remain rather stable and very low (0.5 % and 0.8 % respectively).

3.12. Pescada branca (*Plagioscion squamosissimus*) Fam. Sciaenidae

The pescada branca is a heavy-bodied fish, up to 50 cm long and 3 kg in weight. It is a predatory species, feeding on freshwater shrimps and fishes. Spawning seems to occur in shoals, although the species does not migrate over long distances. Eggs ripen in batches. Spawning occurs throughout the year (WORTHMANN 1982). 2 similar species with the same behaviour are common around Manaus (*P. squamosissimus*, *P. monti*). They are highly prized market species, but comprise only 3 % of the fish sold on the Manaus market (ANNIBAL 1983).

Data for 1977 and 1978 are available on whole fish and fillets (Fig. 14).

No clear seasonality is detected in any of the analyzed parameters. Average water content of whole fish fluctuates between 76 % and 80 %, protein content between 16 % and 19 %, fat content between 0 and 3 % and ash content around 2 %. Average water content of fillets varies between 78 % and 82 %, protein content between 17 and 20 %. Average fat content is < 2 % and ash content about 1 %.

3.13. Other species

26 other species have been sporadically analyzed between 1977 and 1981. Data are given in Tab. 3. Adult females and their gonads, and adult males of the cubiu were analyzed in February and July 1985 (Table 4).

The listed species belong to different taxonomic categories and represent all trophic levels. Many of them belong to the group of "piracema" species, e. g. dourado, piramutaba, pirapitinga, tambaqui, filhote, surubim, cubiu, orana, matrinhã, jaraqui escama fina, branquinha peito de aço and branquinha cascuda. Some others are known to migrate less and to show parental care for eggs and juveniles, e. g. pirarucú, aruanã and acari bodó. There is no detailed information available on the behaviour of the other species.

Some species are economically very important, e. g. the pirarucú and the tambaqui. In 1984 the tambaqui contributed 12 % of the total fish sold on the Manaus market. Aruanã, pirapitinga, matrinhã, surubim and dourado are frequently sold on the market. The piramutaba, is of particular importance in the lower Amazon and the delta area.

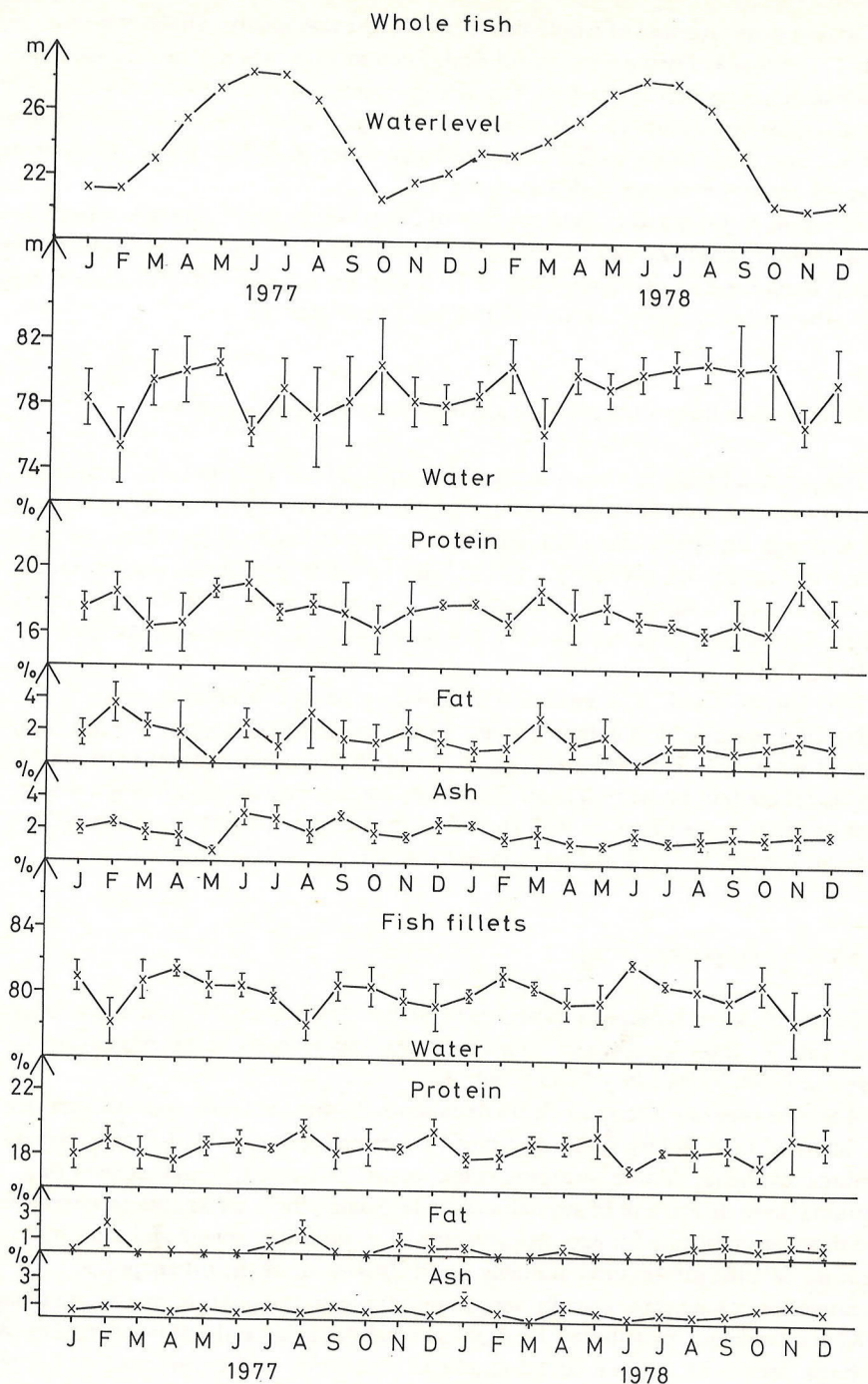


Fig. 14:
Water-, protein-, fat- and ash content of pescada branca (*Plagioscion squamosissimus*) and its fillet in comparison with the waterlevel in 1977/78. (Whole fish: 40 ♂ 80 ♀; total length 20 - 46 cm, \bar{x} = 28.7 cm; weight 90 - 1050 g, \bar{x} = 304 g. Fillet: 55 ♂ 65 ♀; total length 23 - 51 cm, \bar{x} = 31.7 cm; weight 120 - 1690 g, \bar{x} = 437 g).

Tab. 3: Mean values and standard deviations of water-, protein-, fat- and ash content of some Amazonian fish and/or fillets. Number of analyzed ♂♂ and ♀♀, ranges in size (total length) and weight, and month of collection are given for clearer interpretation.

Name	n	Part	Length cm	Weight g	Month	Water %	Protein %	Fat %	Ash %
Acarí-Bodo	2 ♂ 13 ♀	Fillet	29 - 38 \bar{x} 34.1	200 - 810 \bar{x} = 364	5,6,11	85.2 ± 2.0	14.1 ± 1.8	0.1 ± 0	0.6 ± 0.2
<i>Pterigoplichthys multiradiatus</i> Fam. Loricariidae	4 ♂ 1 ♀	Total	60 - 64 \bar{x} 61.4	1190 - 1850 \bar{x} = 1408	7	75.2 ± 2.6	19.8 ± 0.6	2.6 ± 1.6	2.4 ± 0.6
Aruana	7 ♂ 3 ♀	Fillet	55 - 73 \bar{x} 65.2	a 40 - 2350 \bar{x} = 1640	7,12	80.3 ± 0.6	19.0 ± 0.6	< 0.1 ± 0.1	0.7 ± 0.1
<i>Osteoglossum bicirrhosum</i> Fam. Osteoglossidae	9 ♂ 5 ♀	Fillet	31 - 66 \bar{x} 43	660 - 3120 \bar{x} = 1296	5,6,10,11	85.2 ± 1.0	14.1 ± 0.9	0.3 ± 0.3	0.4 ± 0.1
Bacú-pedra	2 ♂ 13 ♀	Fillet	30 - 53 \bar{x} 43.3	400 - 1280 \bar{x} = 741	1,2,8,11	74.6 ± 6.0	20.1 ± 4.9	4.7 ± 2.8	0.7 ± 0.2
<i>Lithodoros dorsalis</i> Fam. Doradidae	9 ♂ 15 ♀	Total	19 - 27.5 \bar{x} 21.9	130 - 460 \bar{x} = 227	3,4,5,8,9	72.0 ± 6.8	18.1 ± 2.0	7.5 ± 5.8	2.4 ± 0.6
<i>Hypophthalmus fimbriatus</i> Fam. Hypophthalmidae	9 ♂ 15 ♀	Fillet	18 - 27 \bar{x} 19.2	90 - 280 \bar{x} = 174	3,4,5,8,9	79.5 ± 1.8	18.8 ± 1.1	0.9 ± 1.0	0.7 ± 0.3
<i>Branquinha cascada</i> Fam. Curimatidae	16 ♂ 15 ♀	Total	20 - 30 \bar{x} 26.5	70 - 420 \bar{x} = 263	1,3,4,8,9, 11,12	74.5 ± 3.3	18.0 ± 1.7	5.2 ± 3.4	2.4 ± 0.6
<i>Pectrogaster rutiloides</i> Fam. Curimatidae	15 ♂ 15 ♀	Fillet	20 - 30 \bar{x} 26.4	70 - 450 \bar{x} = 271	3,4,8,9, 11,12	80.3 ± 1.0	18.5 ± 0.9	0.3 ± 0.2	0.9 ± 0.5
Branquinha peito de aço	3 ♂ 23 ♀	Total	22 - 33 \bar{x} 25.9	69 - 380 \bar{x} = 139	1,2,3,5, 10	73.3 ± 7.0	16.7 ± 0.9	8.8 ± 7.0	1.2 ± 0.4
<i>Potamorhina pristigaster</i> Fam. Curimatidae	5 ♂ 21 ♀	Fillet	23.5 - 33 \bar{x} 26.6	90 - 350 \bar{x} = 147	1,2,3,5, 10	75.0 ± 4.6	18.2 ± 0.9	6.1 ± 4.9	0.7 ± 0.3
<i>Anodus melanopogon</i> Fam. Curimatidae	32 ♂ 37 ♀	Fillet	33 - 85 \bar{x} 57.5	400 - 6050 \bar{x} = 2847	1 - 12 monthly	81.9 ± 1.1	17.0 ± 1.0	0.4 ± 0.4	0.6 ± 0.2
Cuiú-Cuiú									
<i>Oxydoras niger</i> Fam. Doradidae									

Tab. 3: Continuation.

Name	n	Part	Length cm	Weight g	Month	Water %	Protein %	Fat %	Ash %
Dourado	1 ♂ 6 ♀	Fillet	54 - 80 x̄ 71.6	1400 - 3790 x̄ = 3046	2,3,4, 6,10	80.4 ± 1.4	18.3 ± 1.0	0.6 ± 0.8	0.7 ± 0.2
<i>Brachyplatystoma flavicans</i> Fam. Pimelodidae									
Filhote	6 ♂ 28 ♀	Fillet	45 - 78 x̄ 63.7	730 - 4500 x̄ = 2450	1,2,3,4, 6,8,9, 10,11	80.8 ± 1.3	17.9 ± 1.0	0.6 ± 0.7	0.7 ± 0.2
<i>Brachyplatystoma filamentosum</i> Fam. Pimelodidae									
Jaraqui escama fina	7 ♂ 18 ♀	Total	24 - 36 x̄ 29.8	152 - 800 x̄ = 387	2,3,8,9, 10	72.0 ± 4.1	18.1 ± 2.3	8.2 ± 4.9	1.7 ± 0.6
<i>Semaprochilodus taeniurus</i> Fam. Curimatidae									
Jundiá	9 ♀	Fillet	44 - 58 x̄ 52.9	910 - 1930 x̄ = 1463	3,9,11	78.0 ± 1.6	17.9 ± 0.6	3.5 ± 1.9	0.6 ± 0.2
<i>Leiarius</i> sp. Fam. Pimelodidae									
Mandi comum	7 ♀	Total	20 - 25 x̄ 22.4	100 - 230 x̄ = 136	4,7,10	74.0	14.6	10.2	1.3
<i>Pimelodus blochi</i> Fam. Pimelodidae	16 ♂ 23 ♀	Fillet	16 - 28 x̄ 20.8	40 - 220 x̄ = 110	3,4,5,6,7, 10,11,12	80.4 ± 3.6	17.2 ± 2.8	1.7 ± 2.1	0.5 ± 0.2
Mandi peruano	2 ♂ 2 ♀	Total	21 - 25 x̄ 22.8	90 - 140 x̄ = 110	6	64.5 ± 2.6	14.6 ± 0.6	19.9 ± 2.8	1.0 ± 0.5
<i>Auchenipterus nuchalis</i> Fam. Auchenipteridae	4 ♀	Fillet	23 - 36 x̄ 24.8	120 - 150 x̄ = 138	6	74.4 ± 3.2	17.9 ± 0.7	7.5 ± 3.7	0.3 ± 0.1
Mandi porquinho	3 ♂ 2 ♀	Total	15 - 21 x̄ 22.0	50 - 120 x̄ = 136	5	72.4 ± 1.7	15.6 ± 1.5	10.0 ± 2.4	2.1 ± 1.0
<i>Hassar</i> sp. Fam. Doradidae	2 ♂ 2 ♀	Fillet	14 - 17 x̄ 16.0	60 - 70 x̄ = 63	5	79.6 ± 0.9	16.5 ± 0.8	3.5 ± 0.7	0.4 ± 0.1
Mandubé	7 ♂ 5 ♀	Total	27 - 47 x̄ 37.5	200 - 810 x̄ = 560	3,6,7	80.8 ± 2.3	14.9 ± 1.1	4.0 ± 1.5	1.2 ± 0.6
<i>Ageneiosus</i> sp. Fam. Ageneiosidae	9 ♂ 9 ♀	Fillet	20 - 49 x̄ 38.2	350 - 770 x̄ = 565	1,3,6,7	81.3 ± 2.2	16.0 ± 0.7	2.3 ± 1.7	0.5 ± 0.2
Matrinchã	12 ♂ 17 ♀	Total	23 - 46 x̄ 40.4	180 - 1450 x̄ = 1035	1,2,5,6, 8,10	65.2 ± 4.6	17.9 ± 1.8	15.2 ± 5.1	1.8 ± 0.5
<i>Brycon cf. melanopterus</i> Fam. Characidae	13 ♂ 17 ♀	Fillet	28 - 49.5 x̄ 39.0	400 - 1900 x̄ = 1185	1,4,5,6, 8,11	75.9 ± 2.7	19.5 ± 1.1	3.9 ± 2.4	0.7 ± 0.2

Tab. 3: Continuation.

Name	n	Part	Length cm	Weight g	Month	Water %	Protein %	Fat %	Ash %
Muela	4 ♂ 6 ♀	Fillet	24 - 42 x̄ 35.9	200 - 650 x̄ = 446	3,4,8	70.9 ± 6.5	15.1 ± 1.4	13.6 ± 7.3	0.4 ± 0.2
<i>Pimelodina flavipinnis</i> Fam. Pimelodidae									
Orana	3 ♂ 2 ♀	Total	25.5 - 28 x̄ 26.4	160 - 220 x̄ = 196	7	65.4 ± 2.0	16.8 ± 0.5	16.6 ± 1.8	1.2 ± 0.2
<i>Hemiodus unimaculatus</i> Fam. Hemiodidae	4 ♂ 6 ♀	Fillet	26 - 31 x̄ 28.5	200 - 310 x̄ = 249	1,7	75.0 ± 1.0	19.4 ± 1.0	4.9 ± 1.3	0.7 ± 0.2
Piracatinga	2 ♂ 22 ♀	Total	28 - 36 x̄ 32.3	250 - 600 x̄ = 425	5,7	72.5 ± 4.6	13.9 ± 1.4	12.9 ± 5.4	0.8 ± 0.3
<i>Calophrys macropterus</i> Fam. Calophysidae	2 ♂ 22 ♀	Fillet	25 - 46 x̄ 36.4	150 - 870 x̄ = 502	1,3,4,5, 7,8	74.6 ± 6.4	16.3 ± 1.2	8.6 ± 7.1	0.4 ± 0.2
Pirautaba	2 ♂ 9 ♀	Fillet	46 - 68 x̄ 54.3	830 - 1570 x̄ = 1147	4,8,10,12	76.0 ± 3.0	18.6 ± 1.3	4.8 ± 2.8	0.6 ± 0.2
<i>Brachyplatystoma vaillantii</i> Fam. Pimelodidae									
Piranha cajú	4 ♂ 1 ♀	Total	17 - 21 x̄ 19.2	140 - 300 x̄ = 226	9	71.7 ± 3.0	17.5 ± 0.3	7.8 ± 2.7	3.0 ± 0.9
<i>Serrasalminus nattereri</i> Fam. Serrasalminidae	1 ♂ 14 ♀	Fillet	18 - 32 x̄ 27.4	160 - 640 x̄ = 552	1,5,9	80.0 ± 1.2	17.8 ± 1.1	1.2 ± 0.5	1.1 ± 0.3
Pirapitinga	5 ♂ 13 ♀	Fillet	38 - 53 x̄ 46.3	1200 - 3500 x̄ = 2512	2,6,9,10	79.6 ± 1.0	19.1 ± 0.7	0.5 ± 0.4	0.8 ± 0.3
<i>Colossoma bidens</i> Fam. Serrasalminidae									
Pirarara	8	Fillet	53 - 84 x̄ 65.5	3630 - 7960 x̄ = 5293	5,6,11	79.9 ± 0.8	19.2 ± 0.8	0.2 ± 0	0.7 ± 0.1
<i>Phractocephalus hemiliopterus</i> Piracú	19	Fillet	?	?	4,6,7, 11,12	80.8 ± 1.1	18.6 ± 1.0	0.1 ± 0.1	0.5 ± 0.2
<i>Arapaima gigas</i> Fam. Osteoglossidae									
Sardinhão	3 ♂ 7 ♀	Fillet	36 - 48.5 x̄ 43.3	450 - 1220 x̄ = 906	9,10	72.9 ± 4.5	19.8 ± 0.9	6.4 ± 4.3	0.9 ± 0.2
<i>Pellona castelheana</i> Fam. Clupeidae									
Surubim	15 ♂ 47 ♀	Fillet	38 - 77 x̄ 57.0	500 - 3810 x̄ = 1407	monthly	80.8 ± 1.3	18.3 ± 1.0	0.3 ± 0.3	0.6 ± 0.2
<i>Pseudoplatystoma fasciatum</i> Fam. Pimelodidae									

Tab. 3: Continuation.

Name	n	Part	Length cm	Weight g	Month	Water %	Protein %	Fat %	Ash %
Tambaqui ad. <i>Colossoma macropomum</i> Fam. Serrasalimidae	32	Fillet	50 - 85 \bar{x} 71.1	3800 - 11300 \bar{x} = 7171	1,2,3,7,8	79.2 ± 2.0	18.5 ± 1.3	1.5 ± 1.4	0.9 ± 0.4
Tambaqui juv. <i>Colossoma macropomum</i> Fam. Serrasalimidae	46	Fillet	18 - 48 \bar{x} 35.8	350 - 2710 \bar{x} = 1181	1,3,4,5, 7,8,9,10, 11,12	81.3 ± 0.9	17.8 ± 0.9	0.2 ± 0.2	0.3 ± 0.3

Tab. 4: Size, weight and chemical composition of adult cubiu (*Anodus melanopogon*) whole, fillet and ♀ gonads.
Month of capture: February and July 1985. n = 5 specimens for each category. ♀ gonads in July and ♂ gonads in February and July were not analysed because of their small size.

		♂			

4. Discussion

4.1. Limitations of the methodology

Fat is the major energy source in animals of high metabolic activity although in fish glycogen and protein are additional energy sources (SCHUL'MAN 1974). Fish are able to store fat in various ways e. g. in the liver, in the abdominal cavity, subcutaneously, in the muscles, in the interosseous tissue, in the bones and at the base of fins. Thus, analysis of whole fish will provide fuller information on the nutritional status of the fish than the analysis of a single part of its body. This is easily shown by comparing data on whole fish and fillets. In the majority of species fluctuations in the fat and water content are at least twice as high in whole fish as in fillets. On the other hand it is rather difficult, and expensive, to homogenise a 15 kg tambaqui or a 50 kg pirarucú to obtain 5 g fresh material for chemical analysis. Hence fillets or parts of it were analysed. Furthermore, fillet analysis provided information of practical value. Fish is the main source of animal protein for the Amazonian population, and is chiefly consumed as fillets. To date, however, only little data are available on their chemical composition, which is of fundamental interest for both consumer and industrial fish processing companies.

A source of error is present in whole fish processing and analysis when gut content is included. As it was rather difficult to remove gut contents without losing a considerable amount of fat stored around the intestines only full stomachs were emptied before homogenisation. The greater error occurs in the protein content, which is calculated as the difference between wet weight and water-, fat-, and ash content. This is however a generalization which tends to overestimate protein content, as glycogen content for instance is included. Most authors calculate protein content by multiplying total nitrogen, determined by the Kjeldahl method, by a factor of 6.25. According to VAN DE VELDE (1946) the factor for fish should be about 8, whereas DIETRICH (1954) proposes 5.72. DEAS & TARR (1949) show that certain fish proteins e. g. milt, contain more than 16 % nitrogen, whereas others contain less than 15 % e. g. flesh of cod, herring and white spring salmon. JACQUOT (1961) stresses that a general rule cannot be established, but that the conversion factor of 6.25 provides quite good correspondence (MITRA 1956; SCHUL'MAN 1974).

Variation in ash content is of little significance, because the whole fish processing did not homogenize the skeleton adequately. Ash content of fillets is influenced by the individual's ability to avoid cutting bones in the body cavity.

In the vast Amazon basin individuals of the same fish species live under different ecological and hydrological conditions, which may influence their nutritional and/or physiological conditions. Professional fishermen bring the fish from distant areas to the Manaus market; sometimes these areas are more than 1000 km away, and timing of the hydrologic period may differ by 4 weeks, in either direction from that in Manaus. This time lag may be increased or reduced by another month, as a result of the travelling time of the vessels, which are away for up to 6 weeks.

At first therefore I tried to obtain recently caught fish from a single area. This proved however, to be both difficult and very expensive. At certain times migratory species are rarely represent in a given place, and are even difficult to obtain on the Manaus market. Because of the many technical problems I had to use material of different, and in part unknown origins.

In addition, even with specimens from a given place, marked individual differences are to be expected. One part of the stock may have already spawned, another is still preparing to do so, and a third may not spawn at all. Age, size and sex may influence the nutritional status of a specimen, as do parasites and disease. Juvenile specimens seem to utilize most of the energy for rapid growth, adult specimens of some species accumulate fat for spawning. According to LEGENDRE (1938) the immature sardine has about 3 % fat for the first two years of its life. When it reproduces at the end of the third year, fat content oscillates between 5 % and 15 % according to season.

Sex differences are reported to occur in some species, e. g. in cod, regardless of the state of sexual maturity, but in other species, e. g. Baltic herring (KORDYL 1951) no relationship exists between sex and the composition of the flesh.

The effect of specimen selection is shown as well by the rather low standard deviations in the analyses of mature males and females and their gonads, in comparison with data obtained from unselected specimens.

However such a procedure requires many more specimens and many more analyses. I limited selection, excluding juvenile specimens whenever possible, thus obtaining information about the status of the entire adult population at a given period. Because of the great number of variables which may influence the chemical composition of the fish, data will be discussed rather cautiously, only attempting to show general tendencies. Additional studies on selected specimens are necessary to resolve specific aspects of the relationship between the chemical composition and physiological status of fish, and the environmental conditions.

4.2. Relationships between the flood cycle, fish behaviour and their fat-, water-, protein- and ash content

Differences in water-, fat- and protein content between fish species are well known from other regions of the world. Salmon and tuna are considered fatty fish, perch and mullet semifatty and smelt and plaice lean. Variations within a single year are recorded for salmon (0.35 - 14 % fat), herring (2 - 22 % fat), sprat (5 - 18 % fat) and many others (JACQUOT 1961).

Seasonal changes are related to many factors, the principal ones being feeding conditions and the stage of sexual development. According to VENKATARAMAN & CHARI (1951), the Indian mackerel has highest fat levels in the period when plankton is most abundant. Frequently, maximum fat content is reported prior to spawning, particularly for migratory species. e. g. salmon and shad. When these species return from the spawning places they have sometimes lost more than half of their weight and the flesh is of poor quality. It is however difficult to distinguish between the influence of sexual development and nutrition, since the fish do not feed during the spawning period.

The Amazonian fish species investigated throughout the study period can be divided into two categories: Species with strongly — or with weakly — developed seasonality in fat- and water content.

4.2.1. Species with strongly developed seasonality in fat- and water content

This first category includes sardinha comprida (*Triportheus elongatus*), jaraqui escama grossa (*Semaprochilodus insignis*), curimatã (*Prochilodus nigricans*), pacu branco (*Mylossoma duriventris*), branquinha cabeça lisa (*Potamorhina* cf. *altamazonica*) and branquinha comum (*Potamorhina latior*). The species belong to different suprageneric taxa. Average maximum fat content of whole fish may reach 16 to 30 %, whereas minimum fat content can fall to between 1 % and 10 % according to species. The difference between absolute maximum and minimum for individual specimens is even greater.

Water content varies inversely with fat content. In vertebrates, excess fat is generally acquired at the cost of water in the tissue. "Fat-water lines" (LOVE 1970) are given for many fish. Fat content e. g. in halibut, ranges from 0.5 % to 9.6 % while protein content remains constant, at about 18 % (JACQUOT & CREACH 1950). In growth experiments with juvenile carp, fat and water content variation was closely related while protein content remained rather constant (KAUSCH & BALLION-CUSMANO 1976). Protein is consumed only after fat reserves have been utilized during periods of severe starvation, as shown for pink salmon (PARKER & VANSTONE 1966).

Protein content of the adult Amazonian fish studied here also seem to be rather stable. Average protein values vary between 17 and 20 % over one year, absolute maxima and minima of individual specimens being slightly greater (16 - 21 %). The mapará (*Hypophthalmus edentatus*) has lower protein values, 13 - 16 %, probably because of its extremely high fat content.

The seasonality in fat and water content is also often shown in the chemical composition of fillets. However, differences are less pronounced and reach only half or even less of the range shown by whole fish. In the mapará ranges of 30 % in fillets may be almost as high as in whole fish. CARVALHO (1980) accounts for the extremely high fat content in the muscle by the lack of a swim bladder. The mapará, a pelagic species may need high levels of fat in the muscles to reduce its specific gravity. Its abdominal cavity is extremely small and therefore unsuitable for additional fat storage. A rather high fat content in fillets is also shown by the pacu branco (*Mylossoma duriventris*), which has a rather small abdominal cavity, too. Other species e. g. the curimatã (*Prochilodus nigricans*) show little seasonality in fillets which are lean throughout the year fat being stored in other parts of the body.

All species in this group have their lowest fat concentration and highest water content at periods of low water. At this time food availability is lowest — except for predatory fish — and gonad development is advanced. Female gonads are proportionally large, up to 15 - 25 % of the body weight. Their protein content is comparatively high (30 - 40 %) whereas the fat content is relatively low, between 2 - 7 % in the species studied. This indicates that a great part of the fat stored during high water, is used to develop the gonads. Due to the high protein content of the large gonads, females of some species have considerably higher protein but lower water content during this period than the males.

The male gonads are very small contributing less than 1 % to body weight, but nevertheless fat content in males drops to similarly low levels. This shows that a considerable part of the fat stored at high water is used to satisfy energy requirements during falling and low water. Energy balance differences between males and females need further detailed investigation.

Energy requirements are great during spawning season because all species with strong seasonal variation in fat and water content are known to migrate, although probably on different scales. The best known, and very complex, migratory pattern is that of the jaraquis (*Semapochilodus insignis*, *S. taeniurus*). According RIBEIRO (1983) adult jaraquis form shoals when the waterlevel decreases, migrating several hundred kilometres downstream to the Amazon from their feeding grounds in the flooded forest of black water rivers. Final gonad development is triggered by heavy rainfall and the first rise of the river. Migration and gonad development are slower or cease, when the water rise is only slow or if waterlevel begins to fall again (repique). Such hydrologic conditions may delay or extend the spawning period, whereas a rapidly rising waterlevel has a very strong trigger effect, producing a short spawning period and almost simultaneous spawning of the whole population. Contrasting spawning behaviour may explain a prolonged period of low fat content in one year, but a short one in another year, as shown by sardinha comprida (*Triporthus elongatus*) in 1977 and 1980 respectively. However this hypothesis requires further analytical support.

All the species in this group spawn prolifically once a year only. As is no parental care for eggs and juveniles, spawning activity for the individual is rather short, but the spawning season of the entire population lasts several weeks or even months. Specimens exhibit different stages of maturity at the same time, as shown by the very large standard deviations in data at that period.

After spawning fish utilize the abundant food resources of the gradually submerging floodplain and replenish their fat resources within a few weeks correspondingly reducing their water content. At high waterlevel species exhibit their highest fat- but lowest water content. The fall in waterlevel is rather rapid, forcing the fish to retreat from the floodplain to permanent water bodies and the main channel, where crowding ensues, and food resources become less diverse and less abundant (GOULDING 1980).

In addition to the species already mentioned, the following (see Table 3) can probably also be included in this category. Several mandis (*Pimelodus blochi*, *Auchenipterus nuchalis*, *Hassar* sp.), piramutaba (*Brachyplatystoma vaillanti*), sardinhão (*Pellona castelneana*), barba chata (*Hypophthalmus fimbriatus*), piranha cajú (*Serrasalmus nattereri*), piracatinga (*Callophrys macropterus*), cubiu (*Anodus melanopogon*), orana (*Hemiodus unimaculatus*), matrinhã (*Brycon* cf. *melanopterus*), branquinha cascuda (*Psectrogaster rutiloides*), and branquinha peito de aço (*Potamorhina pristigaster*). The sporadic available data show relatively high mean fat content in whole fish and often in fillets too, with a rather large standard deviation indicating pronounced seasonality. The behaviour of these species is however still poorly known. Many are known to migrate and to spawn prolifically e. g. the cubiu (Table 4).

Several large species e. g. the tambaqui (*Colossoma macropomum*) and the pirapitinga (*Colossoma bidens*) are well known migratory species with huge accumulations of body cavity fat. This fat is so abundant in adult tambaqui and pirapitinga that it is used for frying by the local population. According to CASTELO (1979) at high water adult tambaqui accumulate 10 % of its weight as body cavity fat. Data on fillets indicate they are lean, with less than 5 % fat content.

A similar situation may exist for the caparari (*Pseudoplatystoma tigrinum*) and other big catfish. Due to their spawning and migratory behaviour these seem to belong to the "piracema" group. Homogeneously low fat content of fillets may be compensated by great amounts of fat stored in the liver and/or the body cavity, as observed e. g. in the pirarara (*Phractocephalus hemiliopterus*).

A third strategy is also possible when large predatory fish are concerned. Considering that at low water fish are crowded together in the remaining water bodies, an adequate food supply is available to predatory species and they have no need to accumulate large fat reserves. Further observations are however necessary to answer these questions.

According to STANSBY (1961), fish can be classified with respect to their fat content: fatty = more than 15 % fat, semifatty = 5 - 15 % fat and lean = less than 5 % fat.

When whole fish are considered, most of the migratory species belong, at least periodically, to the fatty and semifatty fish. During spawning season however, even very fatty species may have to be considered lean. Some of the migratory species belong to the lean category throughout the whole year, when fillets only are considered.

4.2.2. Species with weakly developed seasonality in fat- and water content

The second category comprises tucunaré açú (*Cichla ocellaris*), acara açú (*Astronotus ocellatus*) and pescada branca (*Plagioscion squamosissimus*).

Average maximum fat content may reach 5 % in whole fish, whereas minimum fat content falls to 0 - 1 %. The difference between absolute maxima and minima in individual specimens can be slightly greater. They belong to the lean fish category.

Water content presents a homologous picture, although this is not as clear as in the first group, because slight fluctuations in protein content may interfere with the relationship. Average protein levels range between 17 % and 19 % over a single year, the absolute maxima and minima of individual specimens being slightly greater 15 - 21 % according to species.

There is little difference between the fat, water and protein content of whole fish and fillets. Lowest fat and protein concentrations and highest water content are attained between the onset of rising water and peak flood. During this period food availability improves steadily but spawning also occurs. The species in this group produce rather small numbers of eggs several times a year. Whereas the pescadas probably exhibit no parental care, the Cichlids protect both eggs and juveniles having well developed territorial behaviour. The gonad weight is much smaller in comparison with the body weight than in the previous group, requiring less energy for its formation.

On the other hand stress is prolonged over the period of egg and juvenile protection with a second and perhaps third spawning act keeping fat content low until peak flood. Spawning seems to end when the waterlevel begins to fall and fish then accumulate small amounts of fat and protein content of fillets increases. According to WORTHMANN (1982) the pescada spawns even during falling water. This, and its predatory behaviour may explain the absence of any seasonality in the analysis.

Whenever possible species of the second group stay in the floodplain. Large scale upstream migration of adults is unnecessary because little downstream drift of juveniles occurs due to the spawning occurring within the floodplain rather than in the main channel, as with members of the first group ("piracema" species).

The data in Table 3 are insufficient to assign other species to the group of fish with weakly developed fat and water content seasonality. The pirarucú (*Arapaima gigas*), the aruanã (*Osteoglossum bicirrhosum*) (Fam. Osteoglossidae) and the acari bodó (*Pterigoplichthys multiradiatus*) (Fam. Loricariidae) show parental care and do not migrate significantly. Available data on fillets indicate they are lean throughout the year, but there are only few data on whole fish (aruanã).

4.2.3. General conclusions

The study deals mainly with some selected species of commercial value which reach a length of greater than 20 cm and a weight of more than 100 g. Therefore any discussion on evolutionary aspects of the development of fat accumulation on a higher taxonomic level would be premature despite the fact that there exists some evidence, that closely related species behave similarly.

For large species however it seems valid that species which migrate and spawn huge amounts of eggs in a single spawning act ("piracema" species) tend towards large temporary fat accumulation. Non migratory species, which often spawn small portions of eggs several times in a year are lean and show little or no seasonality in the fat content throughout the year.

Migratory fish are numerous in species and specimen, representing the bulk of the fish biomass in Amazonian floodplains. About 90 % of the fish sold on the Manaus market belong to this category. Non migratory fish are less abundant. Consequently the accumulation of large amounts of fat during the high water period, when food supply is abundant, furnishing energy for gonad development and spawning migration during low water period, when food supply is limited, can be considered a very successful adaptation to the huge, periodical waterlevel fluctuations in Amazonian floodplains.

5. Summary

Water, fat, protein and ash content was studied in 40 fish species, belonging to 32 genera and 16 families. 10 species were analyzed over one year on a monthly basis, and 4 over 2 years. In all 2548 fish were analyzed.

The chemical composition of the fish varied widely, according to species and, in most cases, the time of year. In general, water content was higher in fillets than in whole fish, whereas fat and ash content were higher in the latter. Protein was on average slightly higher in fillets.

The great majority of the species analyzed, showed a pronounced seasonality in chemical composition, whereas only few species remained rather stable with respect to the analyzed parameters.

Species with strongly pronounced seasonality in fat storage are known to migrate to spawn and/or feed, and to deposit a huge number of eggs in a single spawning act per year. Fat accumulation begins in March/April after the spawning season, with maximum fat content attained at high waterlevel, when the flooded area is most extensive and food offer is at its maximum. Lowest fat concentrations occur just before and during the spawning season at low water, when food offer is reduced and energy demand for migration and spawning is greatest.

Species with little or no pronounced seasonality in fat storage are rather stationary. They spawn several times per year, from the onset of rising water until peak flood or even throughout the whole year producing comparatively small numbers of eggs. They are lean, but may show a slight increase in fat and protein as waterlevel falls and spawning period ends.

Since migratory species represent the bulk of the fishbiomass in the Amazon river and its floodplain, periodical fat storage is considered a very successful strategy by which the drastic environmental changes caused by the large monomodal fluctuation in the flood regime of the Amazon river and its big tributaries can be tolerated.

6. Resumo

O conteúdo de água, gordura, proteína e cinza foi estudado em 40 espécies de peixes pertencendo a 32 gêneros e 16 famílias. 10 espécies foram analisadas mensalmente durante 1 ano e 4 durante 2 anos. Um total de 2.548 espécimens foram analisados.

A composição química dos peixes variou bastante em dependência da espécie e, na maioria dos casos, da época do ano. Geralmente, o conteúdo de água era maior no filé, enquanto que o conteúdo de gordura e cinza era maior no peixe inteiro. O conteúdo de proteína era em média um pouco maior no filé.

A grande maioria das espécies ícticas analisadas mostraram uma sazonalidade pronunciada na composição química, enquanto que somente poucos mostraram pouca variação em relação aos parâmetros analisados.

Espécies com sazonalidade bem pronunciada em relação ao acúmulo de gordura são conhecidas por fazerem migrações de desova e/ou tróficas e de serem de desova total (peixes de piracema). O acúmulo de gordura começa em março/abril, após a época da desova, atingindo o máximo no pico da enchente, quando a área inundada e a oferta de alimentos são maiores.

As menores concentrações de gordura encontram-se pouco antes e durante a época da desova, quando a oferta de alimentos é reduzida e a demanda de energia para a migração e desova é muito grande.

Espécies sem ou com somente pouca sazonalidade desenvolvida no acúmulo de gordura, são relativamente estacionárias. Elas desovam várias vezes ao ano, desde o início da enchente até o seu pico ou mesmo durante o ano inteiro, produzindo um número relativamente pequeno de ovos. São magras, porém podem mostrar um leve aumento no conteúdo de gordura e proteína quando o nível de água baixa e a época da desova termina.

Considerando o fato de que as espécies migratórias representam a grande maioria da ictiofauna no rio Amazonas e na sua área alagável, a acumulação periódica de gordura é considerada como uma estratégia altamente eficaz pela qual modificações drásticas do meio ambiente provocadas pelas grandes flutuações do nível do rio Amazonas e dos seus grandes tributários podem ser toleradas.

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9. References

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